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FRANK CAVERS

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WITH ELEVEN PLATES AND TWENTY-TWO FIGURES
IN THE TEXT



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THE DAILY MARCH OF TRANSPIRING POWER AS INDICATED BY THE POROMETER AND BY STANDARDIZED HYGROMETRIC PAPER¹

BY SAM F. TRELEASE AND BURTON E. LIVINGSTON

(With two Figures in the Text)

INTRODUCTION

The transpiring power of plant leaves, which means their ability to give off moisture by transpiration, possesses considerable importance in connection with studies of drought resistance in cultivated crops and in connection with investigations of relative xerophytism in plant forms in general. Also, transpiring power represents the summed total of all the conditions inside the leaf that tend to accelerate or retard transpiration, so that this physiological characteristic of leaves must be subjected to quantitative study before the general principles of the control of water loss from plants may be understood. It is with the diurnal fluctuations of transpiring power that this paper deals, rather than with differences in this power between different plants.

The foliar characteristic here considered may be directly determined in several ways. (1) The entire aerial part of a plant, or an entire branch, may be enclosed in a chamber and the rate of transpiration may be measured for any given set of conditions (temperature, humidity, wind velocity, etc.). If the surrounding conditions remain the same and the rate of water-loss varies from period to period these variations must be due to internal conditions and the different observed rates should be proportional to the various degrees of transpiring power. Many workers have employed this general method, one form having been recently described by Freeman (6). (2) The transpiration rate for a plant or plant part may be determined under ordinary weather conditions, without enclosing it in a chamber, and the external conditions influencing this rate may be measured and summed for each period by means of some form of atmometer. The quotient of the transpiration rate divided by the evaporation rate from the standardized

¹ Botanical contribution from the Johns Hopkins University, No. 45.

instrument should be a measure of the effective internal conditions or transpiring power (8). (3) The power of the leaf surface to give off water to a standard water-absorbing surface may be taken as a direct measure of its transpiring power. Two such absorbing surfaces have thus far been employed, the horn hygroscope of F. Darwin (4) and the hygrometric paper of Stahl (17). The practical difficulties of the second of these two hygrometric methods seem to be more readily overcome than those of the first, and it is Stahl's method, as improved by Livingston (8), that has been used in the present study.

The transpiring power of a given leaf depends, at any hour of the day, very largely upon the condition of the stomata, whether open or closed, and the importance of stomatal condition is so great in the control of this feature that transpiring power and stomatal condition have frequently been supposed to be practically proportional; the degree of transpiring power has been regarded as a measure of stomatal condition, and conversely. It was only with new methods for somewhat refined study that non-stomatal influences in the daily march of transpiring power have been rendered capable of measurement (7, 9, 14, 15). From the work that has been done in this connection it appears that stomatal condition may frequently exert such a preponderating influence upon the daily march of transpiring power that other influences may safely be neglected, especially in the case of plants with very active stomata, growing under external conditions that do not tend too strongly to raise the transpiration rate.

The open or closed condition of leaf stomata has been actually measured at different hours of the day by several workers, among whom may be mentioned Lloyd (11, 12) and Livingston and Estabrook (10). Lloyd perfected a method of measuring the stomatal openings on bits of epidermis stripped from the leaf, and also measured them directly without injuring the leaf. The last two authors referred to employed the Lloyd method of stripped epidermis.

Besides direct observation of the stomata themselves, a very ingenious method designed for estimating the degree of stomatal closure at different hours of the day has been described and used by Darwin and Pertz (5) and the same method has been employed, with improvements, by Balls (2). By means of the porometer, these authors measure the rate at which air passes through the stomata, with a given range of pressure gradient, and deduce therefrom a measure of average stomatal aperture.

The present study aimed to measure the transpiring power of leaves at different hours of the day, by means of standardized cobalt chloride paper, and to compare the values thus obtained with those derived from porometer readings taken at the same hours. It was thought that such a comparison should throw light upon the relative values of the two methods in the

measurement of foliar transpiring power, and also upon the general subject of transpiring power itself.

On account of their flat, smooth leaves, with stomata only upon the lower surface, plants of the Wandering Jew (*Zebrina pendula* Schnizl.) were used in these experiments. They were grown in partial shade in the greenhouse, and were well-supplied with soil water. The temperature, measured upon a thermometer placed among the plants, ranged from a night minimum of about 20° C. to a maximum in the day of nearly 30° C. A standardized cylindrical porous-cup atmometer showed a fluctuation in the hourly rate of evaporation from a minimum of 0.1 c.c. at night to a maximum of 0.5 c.c. late in the afternoon.

THE HYGROMETRIC PAPER METHOD

For the tests with cobalt chloride paper, essentially the same method was used as that described by Livingston (8) and recently employed by Bakke (1). Small squares of thin filter paper, impregnated with cobalt chloride, were dried for a few seconds over a thin metal plate, heated by an alcohol lamp, and immediately applied, by means of little glass clips, to the lower surface of the leaf to be tested. The time (T_l) required for the change in colour (from blue to pink) upon the leaf surface was determined with a stop-watch. The quotient of the time-period (T_e) required for the colour change over the standard evaporating surface at the same air temperature, divided by this time period (T_l) has been called by Livingston the index of transpiring power of the leaf surface in question. This index $\left(\frac{T_e}{T_l}\right)$ expresses the relative power of the leaf surface to give off water vapour, as compared with the standard evaporating surface blanketed by a millimetre of air.

It has heretofore been the practice (Livingston and Bakke, in the papers cited above) to determine the time-period (T_e) for colour change of the paper over the standard evaporating surface for every leaf test, it being supposed that the temperature of the standard surface is approximately that of the surrounding air. This procedure was omitted in this study, excepting in the case of the first series, the method of the calculation of the value T_e , as suggested by Bakke, being here employed. It appears¹ that the length of this time-period T_e is determined, for any slip of paper and for the standard evaporating surface, by temperature alone, the value in question being inversely proportional to the maximum vapour pressure of water corresponding to the given temperature.

To apply this suggestion, each slip of cobalt chloride paper was tested over the standard evaporating surface once for all, in the laboratory, the

¹ See 1. Also see report of Livingston's later work in 13.

time T_e and the prevailing air temperature (t) being recorded in each case. From these data, and from a table of maximum vapour pressures of water, it was possible to calculate approximately the value of T_e for any other temperature. Thus, a simple calculation is here substituted for the rather troublesome experimental determinations of the value T_e as these would have to be made at various hours of the day and night and in the greenhouse. In practice it was found that the final results appear fully as consistent and satisfactory when this procedure is followed as when the papers are actually standardized over the evaporating surface each time when leaf tests are to be made.

The method of calculation may be illustrated by means of the following figures from the present study. The slips of paper used in these tests were found, by many trials over the standard evaporating surface at a temperature of 22.5°C ., to have a nearly constant average period of change, 28.2 seconds. From the preceding discussion it is evident that, if $P_{22.5}$ stands for the maximum vapour pressure of water at 22.5° and if P_t stands for this vapour pressure at t degrees, then the value of T_e for the temperature t [$(T_e)_t$] may be found as follows:

$$\frac{(T_e)_t}{(T_e)_{22.5}} = \frac{P_{22.5}}{P_t},$$

$$\therefore (T_e)_t = \frac{P_{22.5} (T_e)_{22.5}}{P_t}.$$

The value of $P_{22.5}$ is found to be 20.264 mm., from a table of aqueous vapour pressures, and the value of $(T_e)_{22.5}$ was found by laboratory tests to be 28.2 sec., as has been said, from which it appears that $(T_e)_t = \frac{571.44}{P_t}$, and the value 571.44 is a constant for all pieces of paper changing colour in 28.2 seconds over the standard water surface at a temperature of 22.5°C . This constant may be termed the coefficient (K) of the paper with reference to the standard evaporating surface, and if K is known for a given piece of paper the time required for its colour change over the standard surface for any given temperature may be found by dividing the value K by the maximum vapour tension of water for the particular temperature in question.

The index of transpiring power of the leaf surface, as measured by tests with hygrometric paper and in terms of these symbols, is $\frac{T_e}{T_l}$, and this value may be designated as I_H . This index, as has been mentioned, expresses the relative capacity of the leaf surface to transpire, and is directly comparable with other indices similarly determined for the same plant at different times, or for different plants at the same time.

The general applicability of the method of standardized hygrometric

paper rests on the supposition that all the slips of paper used in the comparisons have approximately the same water-absorbing power when placed on the leaf, and that this capacity to absorb water decreases in the same manner in all cases, as the slips become moist. The principle here involved is the same as that employed in Darwin's method of the horn-hygroscope, but to standardize the latter method would be a difficult task. The use of the standardized paper slips also involves, as far as it has yet been worked out, the supposition that the temperature of the slip and of the air lying between it and the leaf is the same as that of the surrounding air, for Livingston's plan of standardizing each slip is based on the proposition that these two temperatures are practically the same. No doubt there is a serious fault in the method here, for a leaf is usually either cooler or warmer than the surrounding air, but this fault cannot be corrected until the measurement of leaf temperature becomes much more readily accomplished than is now the case. In default of a readily workable method for leaf temperature determination it appears that the results so far attainable by means of standardized paper slips make it worth while to neglect this fault, which may be later corrected. The error involved in supposing the leaf to have the temperature of the surrounding air does not appear to have rendered the results thus far obtained inconsistent with what would be expected if this supposition were indeed true, and the error itself may be supposed to be comparatively slight in the case of the present tests, especially since the evaporating power of the air in the experimental greenhouse was never very great and the plants were shaded from direct sunshine.

THE POROMETER METHOD

Practically the same form of porometer was used as that originally described by F. Darwin and Pertz (5). This instrument is considered as giving relative measurements of the average stomatal aperture in terms of the rate at which air may be drawn through the leaf. The tube of a small medicine dropper about 6 mm. in diameter at its larger end was found satisfactory for use as the suction chamber, its flange being cemented to the leaf with warm glue so as to make an air-tight joint. A piece of rubber tubing connects this chamber with one of the horizontal arms of a glass T-tube, the vertical portion of the latter dipping into a vessel of water below. The other horizontal arm bears a piece of rubber tubing closed at the end by a pinch-cock. The vertical tube bears a millimetre scale. After attaching the suction chamber to a leaf, the water in the vertical tube is brought above the zero mark, by compressing the rubber tube and releasing it again, thus forcing a bubble of air out of the lower end of the tube. The water column in this tube then falls slowly, if the stomata are not completely closed, on account

of the entrance into the chamber of air which passes through the leaf. The time (T_p) required for the meniscus of the liquid to fall a suitable distance (4 cm. in these tests) was measured with a stop-watch.

Since it was not necessary in these studies, no attempt was made to calibrate the instrument, the readings being used merely as relative measures. The reciprocal of the time required for the entrance of a given amount of air into the porometer chamber is the rate of air flow $\left(\frac{1}{T_p}\right)$, which may be regarded as a measure of the average cross sectional area of the stomatal pores, following Darwin and Pertz, and Balls. According to the work of Brown and Escombe (3), however, the power of stomata to allow the escape of water vapour from the leaf (the stomatal diffusive capacity of these authors) is proportional to the diameter of the average cross sectional area of the pores, which again is proportional to the reciprocal of the square root of the average porometer time $\left(\frac{1}{\sqrt{T_p}}\right)$, if the stomatal pores are treated as if they were circular in cross section. It is interesting here to note that, while there is good reason for believing that the rate of *diffusion* of gases through stomata is proportional to the *diameters* of circles having areas the same as those of the cross sections of the stomatal pores (Brown and Escombe), it is also clear that the rate of molar *flow* of gas through these same openings is at least approximately proportional to the *areas* of these circles. If the diffusive capacity of the stomata is represented by I_p , then $I_p = \frac{1}{\sqrt{T_p}}$. This diffusive capacity should be a measure of the transpiring power of the leaves in question, *if no factor other than the degree of stomatal opening is influential in determining transpiring power*, and it is this value that is here to be compared with the other index of transpiring power (I_n) derived from the tests with hygrometric paper.

It should be noted that the porometer operates by decreasing the air pressure over a certain group of stomata (those covered by the suction chamber), while the pressure over the other stomata remains unaltered. Thus the instrument actually measures the rate at which air with a certain average pressure gradient moves into the free stomata, through the internal gas spaces of the leaf, and out of the stomata covered by the suction chamber. Darwin and Pertz and Balls have expressed the conviction that this rate of flow is controlled solely by the size of the stomatal apertures, a conclusion that may well be true in the majority of cases, or even always, but which does not directly follow and requires experimental proof. It is clear that the rate of gas flow through an intricate system of passages such as is offered by the interior of the leaf may be influenced by the average cross-sectional area of the passages themselves, as well as by the average size of the openings

through which these passages connect with the outer air. Since many more stomata are available for entrance than for exit of the air current, as the porometer operates, it appears that the size of the free stomatal openings must be without influence on the rate of flow, which may, then, be determined either by the average size of the openings that are covered by the suction chamber, or by the effective size of the internal gas spaces of the leaf. It seems highly probable that the internal spaces may as a general rule be neglected, as the writers above mentioned have tacitly done, but it should be borne in mind that some leaves have relatively small internal gas channels and that no evidence is yet at hand as to whether these channels may or may not alter in cross section as the internal conditions of the leaf (such as water content, soluble carbohydrate content, etc.) vary from hour to hour. In short, the porometer appears to offer a direct means for measuring the resistance offered to gas-flow into a large group of stomata and out of another smaller group, but it does not, in itself and directly, give any information bearing either on the size of the stomatal apertures or upon the ability of the leaf to give off water by transpiration. No method has yet been suggested by which average stomatal aperture may be actually determined, excepting the method of direct micrometer measurement. If porometer readings are to be interpreted as measures of foliar transpiring power or of average stomatal aperture, such interpretations must rest upon experimental evidence of the relation between the rate of air flow (as measured by the porometer), on the one hand, and transpiring power and average stomatal aperture, on the other. It is possible that the kind of plant used, its previous history, and the march of the climatic and soil conditions during the particular day when tests are made, may be influential in determining whether or not porometer readings really indicate relative foliar transpiring power, or even average stomatal aperture, in any particular case.

MEASUREMENTS AND RESULTS

The experiments performed in the present study consisted of nearly simultaneous tests with the porometer and with standardized cobalt chloride paper, upon the lower (stomatal) surface of leaves of *Zebrina pendula*. The observations, usually made at two-hour intervals, were always begun before daylight and were continued until well after sunset. Five or six tests, of different but apparently similar leaves, were made at each time and by each method. For the tests with cobalt chloride paper the leaves were left attached to the plants. For the porometer tests some series were carried out with the leaves still attached, but comparison of the results thus obtained with those derived from severed leaves showed no appreciable difference, and so, for convenience, the leaves were usually detached from the plant just before the porometer was applied.

Daily March of Transpiring Power

To show the nature of the individual readings and the extent of variation, the results of one entire series of tests, made on June 10th, are given in Table I. This table shows a sample of the individual leaf tests with the cobalt chloride paper and with the porometer, and also shows the calculated indices of transpiring power (I_H), and the average stomatal diffusive capacity (I_p) as indicated by the porometer.

TABLE I

Data of relative transpiring power (by standardized cobalt chloride paper) and of relative stomatal diffusive capacity (by porometer) for leaves of Zebrina pendula, June 10th, 1915

Time of observation	3 a.m.	5.30 a.m.	7.30 a.m.	10 a.m.	12 noon	2 p.m.	5 p.m.	8 p.m.
Air temperature, deg. C. (t)	19.0	19.2	19.8	23.6	27.0	29.8	28.0	25.0
Calculated time for colour change of cobalt paper over standard evaporating surface at t° , sec. [$(T_e)t$]	34.9	34.4	33.2	26.4	21.5	18.3	20.3	24.3
Observed time for colour change on leaf, sec (T_l)	528 492 620 608 518 481	388 345 238 302 286 304	225 242 195 188 239 140	201 145 171 154 130 140	138 123 172 150 178 124	140 111 212 144 150 93	252 270 371 281 285 289	506 554 575 584 494 467
Index of transpiring power by hygrometric paper ($\frac{T_e}{T_l} = I_H$) ¹	.066 .071 .056 .057 .067 .073	.089 .100 .145 .114 .120 .113	.148 .137 .170 .177 .139 .237	.131 .182 .154 .171 .203 .189	.156 .175 .125 .143 .121 .173	.131 .165 .086 .127 .122 .197	.081 .075 .055 .072 .071 .070	.048 .044 .042 .042 .049 .052
Average	.065	.114	.168	.172	.149	.138	.071	.046
Time required for 4 cm. fall of water column in tube of porometer, sec. (T_p)	92.4 35.2 21.2 50.0 23.2	5.8 5.6 5.4 4.8 5.6	3.6 4.0 5.4 5.6 3.8	4.8 5.4 3.2 3.4 4.6	8.4 7.6 4.4 3.4 9.2	5.8 8.0 4.8 7.6 6.8	17.4 10.2 24.8 8.2 41.4	54.8 112.0 79.2 144.0 140.0
Index of stomatal diffusive capacity ² , ($\frac{1}{\sqrt{T_p}} = I_p$)	.104 .168 .217 .141 .208	.415 .423 .430 .456 .423	.526 .500 .430 .423 .512	.456 .430 .558 .542 .466	.345 .363 .477 .542 .330	.415 .354 .456 .363 .383	.240 .313 .201 .349 .155	.135 .094 .112 .083 .084
Average	.168	.429	.478	.490	.411	.394	.252	.102

¹ On the supposition that the leaf temperature is the same as that of the air (t°).

² On the supposition that the rate of air movement into the porometer (i.e. the rate of fall of its water column) is proportional to the average cross-sectional area of the stomatal pores, and that stomatal diffusive capacity (capacity to allow outward diffusion of water vapour) is proportional to the diameter of a circle having an area equal to the average cross-sectional area of the pores.

The average values of I_H and I_p obtained from five different series of tests, including that of June 10th, are presented in Table II, but all of each series of values are here expressed in terms of the value for 3 a.m. of the same series, this value being considered as 100. The corresponding actual values are given in parenthesis below the first value in each case. This use of relative values allows direct comparison to be made between the two indices for the same series and between indices of different series. For

TABLE II

Indices of foliar transpiring power for Zebrina pendula, by hygrometric paper and by the porometer

Hour of observation	Hygrometric paper						Porometer					
	I	II	III	IV	V	Aver- age	I	II	III	IV	V	Aver- age
2 a.m. ...	93	—	—	—	—	—	May 8th	May 22nd	June 5th	June 10th	June 16th	—
3 ...	(0-08) 100 ¹	100	100	100	100	100	(0-13) 100 ¹	100	100	100	100	100
4 ...	107	127	92	131	120	115	96	105	108	162	148	124
5 ...	131	153	84	160	138	134	147	110	115	224	196	158
5.30 ...	—	—	—	175	—	—	—	—	—	255	—	—
6 ...	161	204	114	197	197	175	198	146	136	262	238	196
7 ...	182	254	143	238	257	215	207	182	157	277	280	221
7.30 ...	—	—	—	258	—	—	—	—	—	285	—	—
8 ...	202	223	178	260	251	223	216	220	206	286	266	239
9 ...	185	191	210	262	244	218	207	259	254	288	252	252
10 ...	167	213	178	265	271	219	199	255	251	292	275	254
11 ...	163	235	143	248	297	217	219	251	247	269	298	257
12 noon...	159	231	163	229	252	207	239	220	211	245	262	235
1 p.m. ...	140	227	182	221	205	195	218	189	175	240	225	209
2 ...	122	168	150	212	182	167	197	175	145	235	211	193
3 ...	104	107	117	178	159	133	176	160	115	207	197	171
4 ...	83	92	113	143	134	113	150	151	110	178	180	154
5 ...	61	76	109	109	108	93	124	141	105	150	164	137
5.30 ...	—	—	107	—	—	—	—	—	102	—	—	—
6 ...	61	78	—	97	86	81	98	142	—	120	126	122
7 ...	61	81	—	83	64	72	70	143	—	90	89	98
7.30 ...	—	86	—	—	53	—	—	144	—	—	70	—
8 ...	—	—	—	71	—	—	—	—	—	61	—	—

example, the index, by hygrometric paper, for 6 a.m. of Series I is 61 per cent. greater than the index for 3 a.m. of the same series. The corresponding index by the porometer is 98 per cent. greater than the porometer index for 3 a.m., etc. Since the observations were not always made at the same hours interpolations have been made in each series, so as to give the approximate values for every hour. The interpolated values are distinguished from those actually derived from observations by the fact that the former are shown in italics. In the last column of each section of Table II are given the

¹ Numbers in italics have been calculated by interpolation.

mean indices, representing all five series together. Since the environmental conditions did not vary markedly from series to series, and since the series themselves indicate no progressive change in any particular, it appears reasonable to regard these final means as representing what may be expected to be the general relation between the relative hourly values and daily marches of the foliar transpiring power and of the porometer index of stomatal diffusive capacity, as indicated for these plants by the two methods here tested.

The five separate series of hourly index values and the composite series of means (all from Table II) are represented graphically in Figs. 1 and 2, Fig. 1 including the two sets of graphs for each of Series I-III, and Fig. 2 including those for Series IV and V, together with the pair of composite graphs. In these curves the full line represents foliar transpiring power as derived from the tests with cobalt chloride paper, while the broken line represents the corresponding indices derived from porometer readings.

Inspection of the graphs shows that the daily range between the early morning index value and the maximum for the day is always greater for the values derived from porometer readings than for the corresponding ones obtained by the other method. Furthermore, the graph of porometer values shows a marked general tendency to remain above the other graph throughout practically its entire course. Why the case of Series II is a partial exception to this cannot be stated.

The various graphs show numerous irregularities, but there is seen to be a considerable tendency for the same irregularities to appear simultaneously in both graphs of a pair, this being especially marked in the case of Series IV and V. The irregularities of the individual series are practically eliminated in the composite graphs, which present very smooth, round-topped curves. The latter bring out very clearly the generalization mentioned above, that the porometer method shows a greater range in its index values (average stomatal diffusive capacity) than is indicated for the other indices (transpiring power) by the method of standardized cobalt chloride paper, and that the graph of porometer values has the higher position throughout the day. If the composite graphs may be considered as approximating a true representation of the general state of affairs for such plants as these, it may be stated that foliar transpiring power as indicated by the hygrometric paper rises to its maximum a few hours after sunrise, falls slowly till about 1 p.m., and then falls more rapidly to the low night values. As indicated by the porometer readings, on the other hand, the maximum index value occurs several hours later than in the other case and the subsequent fall is much more abrupt.

Some influence is obviously effective within the plant to produce this daily march in both graphs, but this influence is not so effective to increase and maintain the cobalt chloride paper index as it is to increase and maintain

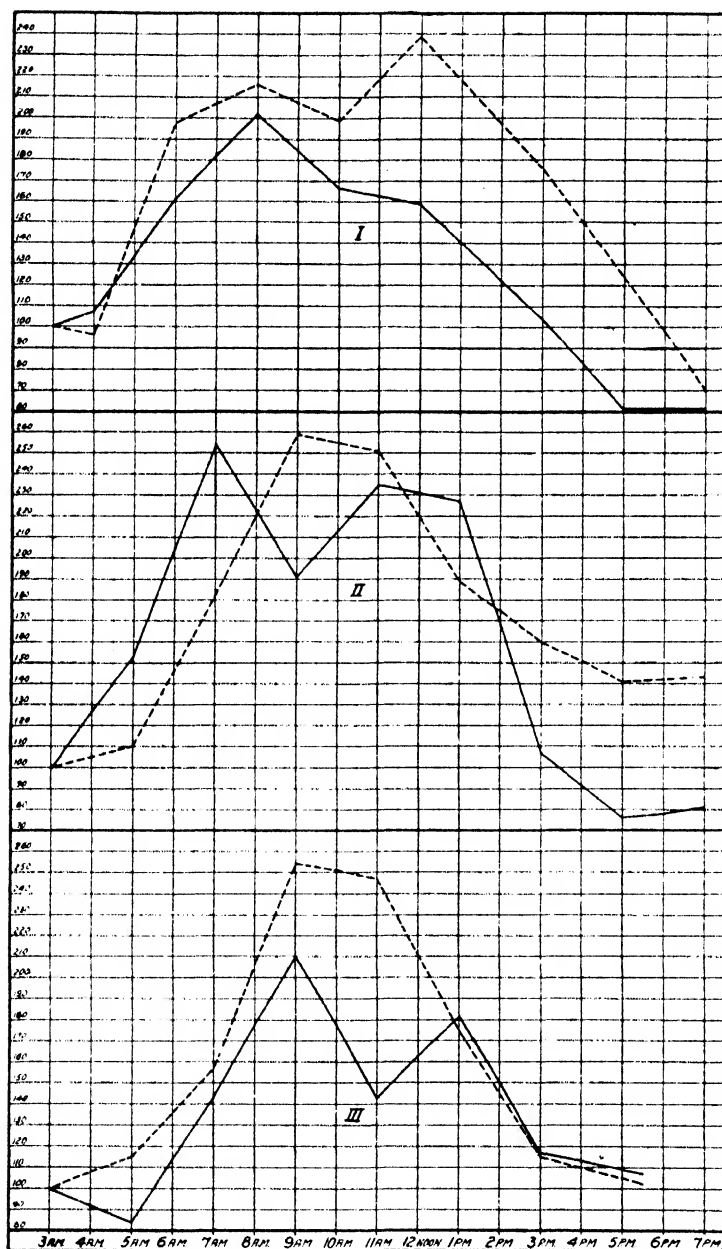


FIG. 1. Graphs of index of transpiring power of lower leaf surface of *Zebrina pendula*, as determined by hygrometric paper (full line) and of average stomatal diffusive capacity, as determined by porometer (broken line). Series I, May 8th; Series II, May 22nd; Series III, June 5th, 1915.

Daily March of Transpiring Power

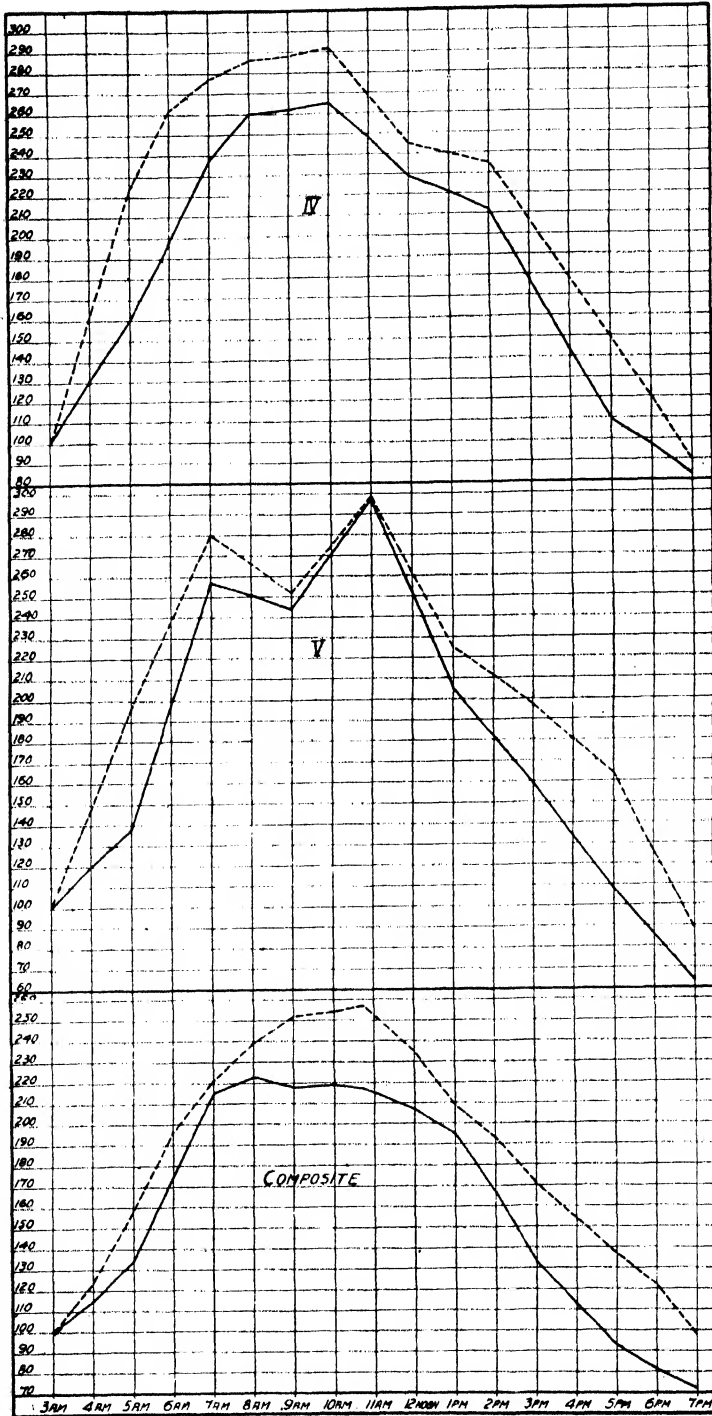


FIG. 2. As Fig 1. Series IV, June 10th; Series V, June 16th. The last graph (composite) represents the averages derived from the five separate series of observations.

the porometer index. Looked at from another point of view, some influence in the plant tends to increase both indices until about 8 a.m. and continues to increase the porometer index until about 11 a.m., but an influence in the opposite direction begins to be apparent in the case of the cobalt index as early as 7 a.m. and is dominant after 8 a.m. After 11 a.m. this reducing influence is clearly dominant in the case of the porometer index also. Assuming that the stomatal diffusive capacity may actually be deduced from the porometer readings, the relation of the two composite graphs strongly suggests that some condition other than this diffusive capacity plays a rôle in determining the index of transpiring power, as the latter is more directly measured by the hygrometric method. Now, aside from the diffusive capacity of the stomata, two other features of the leaf may influence transpiring power, so far as is now known. One of these is the power of inter-stomatal cuticle to give off water, a feature which the porometer method is surely unable to take into account, but to which the method of hygrometric paper should be sensitive. The other is the partial pressure of water vapour in the sub-stomatal spaces of the leaf. Both of these conditions should depend upon the state of saturation of the leaf tissues, and it seems possible that this is the feature that produces the difference between the two graphs in question. Without following this proposition into further detail, it may be suggested that the conception of incipient drying of Livingston and Brown (9), which is essentially the same as that of the saturation deficit of Renner (15, 16), may furnish an explanation of these phenomena. If this be the case, it might be expected that the hygrometric method would detect the influence of incipient drying while the porometer method would fail to do so, which agrees with the indications here brought out by the composite graphs.

From the limited amount of information here available it may, then, be tentatively concluded that the porometer method may furnish a measure of the diffusive capacity of the stomata, but that it may fail to take into account other influences that affect foliar transpiring power, and therefore is not to be expected always to furnish a thoroughly satisfactory measure of the latter. Nevertheless, it is clear that, for the conditions here dealt with and for these plants of *Zebrina pendula*, the two methods *do* give results that are in practical agreement for many purposes, probably because the porometer does furnish a measurement of stomatal diffusive capacity and because this capacity is by far the most powerful influence taking part in the control of foliar transpiring power in such plants as these.

It may be suggested, in conclusion, that the non-stomatal influence affecting foliar transpiring power may be susceptible of approximate measurement by the use of these two methods. If the indices obtained by means of the hygrometric paper are true expressions of transpiring power and if the indices furnished by the porometer readings are measures of the stomatal

influence upon transpiration, then the quotient obtained by dividing the former of these indices by the other, for the same hour, etc., should be an index of the non-stomatal influence. The inadequacy of the data here available, however, seems to render a quantitative test of this suggestion uncalled for in the present connection.

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THE BOTANICAL RESULTS OF A FENLAND FLOOD

By R. H. COMPTON

(With Plates I and II)

The East Anglian Fenland depends for its existence as the most productive agricultural area in England upon the maintenance of the river banks. These were constructed, mainly in Jacobean times, in order to hold up the water-courses and thus to form a drainage system into which the water from the low-lying country could be pumped. Owing to carelessness, exceptionally heavy rains, sinking of the ground-level, or undermining, a bank occasionally gives way, and a flood (or "drown" as it is locally called) takes place: the inundation lasts until the banks have been repaired and the water has been pumped off.

In the early days of January, 1915, such a flood took place on the agricultural land known as Southery, Methwold, Feltwell and Hockwold Fens; the area inundated being about 24 square miles. This area has an altitude of from 2 to 8 feet above sea-level. The soil is a black peat of the type general in Fenland. The water flooding the area was derived from the Little Ouse or Brandon River, which drains the sand-covered chalk uplands of part of the Breckland country; it was thus rich in lime and other mineral salts, as is usual in the Fen District. The depth to which the land was flooded varied with the altitude of the land-surface; in some places the water was about 8 feet deep. The scanty population fled to the uplands to await re-drainage. This was completed in October, 1915, when ploughing operations were resumed.

Thus for about nine months this fenland area was restored to something like its original aquatic conditions. The result of this was, briefly, to extinguish the centuries-old terrestrial flora of cultivated plants or weeds, and to replace it by an aquatic flora derived from the waters of the drainage channels.

1. *Effects on the terrestrial flora*

Trees and shrubs of good size, whose branches emerged from the water, survived. This applies to apple and pear trees in farm gardens, to hawthorn planted as hedges and to the poplars and willows fringing the lodes or ditches. Low hedges of *Buxus*, gooseberries, currants, etc., were killed. The willows (*Salix alba* and *S. fragilis*) responded to the flooded conditions by producing great masses of adventitious roots from the submerged parts of their trunks

and branches. This is shewn in Plate I, Phot. 1, photographed after re-draining.

The herbaceous flora appears to have been almost completely destroyed—that is, as far as growing plants are concerned: some plants may have survived in the form of seed. The only terrestrial plants which seem to have lived through the whole flood were *Cochlearia armoracia* (horseradish, planted in farm gardens, whose root-stocks sprouted again after drainage), and *Cnicus arvensis*. Of the latter a few specimens in a remarkable condition were found. At first sight the leaf-rosette appeared normal (November, 1915); but on lifting it, it was found to be attached to the ground by about 2 or 3 feet of slender leafless stem of very soft and flexible consistency—exactly resembling the woodless stem of a true aquatic. During the flood *Cnicus arvensis* had evidently floated at the end of this aquatic stem, much in the manner of, say, a *Potamogeton* or *Callitriche*.

With these exceptions, the whole terrestrial flora seemed to have been extinguished. The number of seedlings which had appeared a month or six weeks after re-drainage was unexpectedly small; a few young plants of *Agrostis stolonifera* and *Agropyrum repens* were establishing themselves, but whether the seeds or rhizomes had remained dormant under water or seeds had been introduced subsequently was not discovered.

2. *Invasion of an aquatic flora*

The state of affairs disclosed by the re-drainage afforded a striking demonstration of the rapidity and completeness of the invasion by a new flora of an area suddenly rendered available to it. The greater part of the area was covered to the degree of a “closed association” with one or other of a few typical aquatic or paludal plants. The source of these new arrivals was probably two-fold. Some originated in the low-level ditches with which the district is intersected; of these *Chara hispida* is the most remarkable. Others arrived in the form of spores or seeds carried by the river water as it spread over the land.

The most striking of the invading plants was *Cladophora flavesceus*, which flourished in the flood waters, and when the land was re-drained formed a dense felt-like covering to the ground. It was possible to lift this “blanket weed” (to use the appropriate local name) in large sheets (Plate I, Phot. 2), and so thick was it in some places that it was necessary to rake it off before the land could be ploughed. *Cladophora flavesceus* covered a very large proportion of the flooded area, acres at a stretch, either pure or mixed with *Polygonum amphibium*. The latter occurred in considerable abundance, rooting in the peaty soil, and producing branches often 8 feet long (an indication of the depth of the flood), which bore flowers and seeded freely.



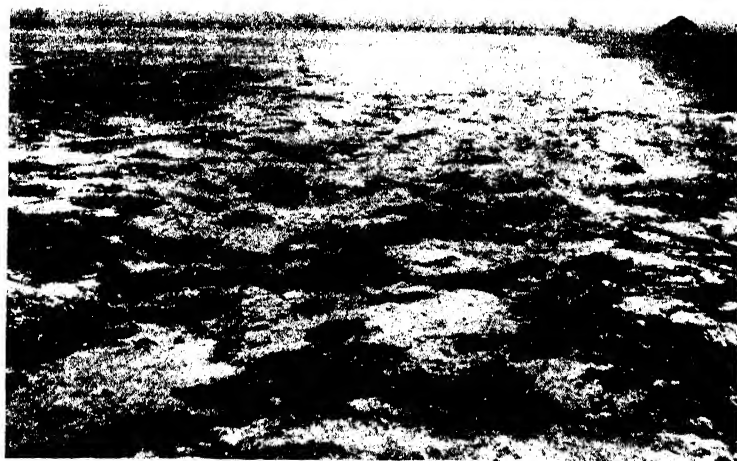
Phot. 1



Phot. 2



Phot. 3



Phot. 4

In many places these plants were so frequent that their leaves must have formed a thick covering to the water.

Another flowering plant, *Alisma plantago*, was present in such local abundance as to form a closed association so dense that even the *Cladophora* was unable to grow amongst it with freedom (Plate II, Phot. 3).

Chara hispida, which occurs normally in the ditches and lodes in Fenland, had seized the opportunity afforded by the flood, and had climbed out of the ditches and formed a zone several feet broad on either side. It is possible that if the flood had been more prolonged the *Chara hispida* would have captured much of the area occupied by *Cladophora flavesceus*. In the zones where it was present it excluded other vegetation, and, when seen after drainage, it formed a thick soft white calcareous mat on the soil (Plate II, Phot. 4).

The four plants mentioned (*Cladophora flavesceus*, *Chara hispida*, *Polygonum amphibium*, *Alisma plantago*) were the most abundant of the aquatic invaders. Several other species however occurred, more or less frequently. These were *Mentha aquatica* var., *Callitriche verna* var., *Veronica beccabunga*, *Typha latifolia*, *Oenanthe fluviatilis*, *Lythrum salicaria*, *Vaucheria terrestris*, *Enteromorpha intestinalis*. These all occurred as isolated plants, never forming a true society.

A few plants, normally growing in the ditches, survived the flood; among these were *Arundo phragmites*, *Glyceria aquatica*, *Rumex hydrolapathum*.

This "natural experiment," comparable with the sterilisation of a Krakatau, gave a striking demonstration of the rapidity and completeness of the invasion of a new adaptive flora. The distribution of the different floristic elements over the area was due to a variety of factors—the abundance of the reproductive bodies of each species, the direction of currents, the relative rapidity of propagation, and so on. The final sub-stable ecological result would certainly be widely different. The first flora of such a newly available area must be opportunist: the ultimate result attained after some years would express in addition the factor of local competition.

DESCRIPTION OF PHOTOGRAPHS ON PLATES I AND II

- Phot. 1. Small tree of *Salix alba* which had produced a great number of adventitious roots from its trunk at and below the flood level.
- Phot. 2. *Cladophora flavesceus* covering the ground, propped up here and there on stubble; capable of being lifted in large sheets. Scattered amongst it are plants of *Polygonum amphibium*.
- Phot. 3. *Alisma plantago* dominant. *Cladophora flavesceus* in the interstices. A single plant of *Veronica beccabunga* in the middle.
- Phot. 4. *Chara hispida* spreading from the ditch on the right of the picture. (Photograph by Mr G. R. Petherbridge.)

THE VEGETATION OF THE TARAWERA MOUNTAIN, NEW ZEALAND

PART I. THE NORTH-WEST FACE

BY B. C. ASTON

(*With Plates III-V*)

On June 10, 1886, New Zealanders were startled from their quiet lives by a volcanic eruption, the sounds of which reached from three to four hundred miles north and south from the seat of the outburst, while ashes fell over an area variously estimated at from 4000 to 6000 square miles. The greatest depth of the matter ejected, measured at the lip of the great vent, was 170 feet, the top of the range being increased by this amount. It has been estimated that from two-fifths to one cubic mile of material was thrown out. The eruption took place along a flat-topped range, 3600 feet in altitude and composed of rhyolitic lava flows, known as Tarawera Mountain and comprising the peaks Wahanga (northernmost), Ruawahia, and Tarawera (southernmost). This range is situated on the eastern side of Lake Tarawera, in the thermal district of the North Island where are situated Lakes Rotorua and Taupo, well known as tourist resorts.

A gigantic rent opened along the axis of the range, running roughly north-east and south-west, commencing at the north end and extending to Tarawera, thence in a line more westerly to Lake Rotomahana, the waters of which are thought to have caused further explosions. This rent finally ended at Lake Okaro in the south, taking but three or four hours to form. See Plates III, IV, Photos. 1, 2.

Along this immense chasm in the earth, nearly 9 miles long, 900 feet deep at its greatest and 300 feet at its least depth, a mile and a half to an eighth of a mile wide, were no less than seventeen points of eruption. The fissure is not continuous but is bridged in several places by the original surface remaining in position. This titanic feature of the North Island thermal district is at the highest points certainly the most impressive of the sights, and probably that least visited by tourists.

The north-western face of the Tarawera Range at present rises from the shores of Lake Tarawera (which is 1032 feet above sea-level) to a height of 2738 feet above it, the summit of the range being 3770 feet above the sea. S. Percy Smith, who had the advantage of thoroughly exploring the



Phot. 1. On the summit of Tarawera, 3700 feet, looking towards the Bay of Plenty, with Mt Edgecumbe in the distance, showing a portion of the rift.



Phot. 2. The Rift on Tarawera Mountain.

This photograph was taken at 3400 feet, and shows a portion of the rift (nine miles in length) formed at the time of the eruption. The white layer (rhyolite) is a rock poor in plant food, but the dark coloured layer of scoria (andesite) on the top is rich in plant food.



Phot. 3. Lower Slopes of Tarawera Mountain.

The mud on the slopes has been cut into channels by the rain, presenting the appearance of ploughed land. The vegetation, the seed of which must have been brought by birds, is chiefly tree tutu (*Coriaria*).



Phot. 4. Slopes of Tarawera, 1450 feet.

In the background is seen the summit of Tarawera, while in the middle distance are seen gullies with the vegetation slowly creeping up the mountain. In the foreground are manuka (*Leptospermum*) and tutu scrub, with patches of Strathmore weed (*Pinchia*).

Phot. 5. Tarawera Lake—Kanchapa Beach.

Showing the dead trees in the foreground killed at the time of the eruption and the recent growth of pohutukawa (*Metrosideros tomentosa*) and other young trees and shrubs.

mountain both before and after the eruption, describes the contour of the mountain as being unlike any other in the district, with the plateau-like summit sloping down to say 400 feet, the steep "mural crown" below descending for say another 400 feet, the sharply-inclined talus at an angle of 30° extending 1000 feet below the rock faces that form the "mural crown," and the beautifully easy slopes lowest of all grading down to the lake margin as a pumice beach or ending in low cliffs at the water's edge. This is a fair average of the aspect it presents on every side except towards the east, where a range of less elevation joins it and spoils its symmetry.

The forests which once clothed the slopes of this mountain, according to this authority, were of considerable extent, especially over the south-eastern flanks (that is, on the opposite side of the range to that described in this paper). The eruption has utterly destroyed these forests. One instance of a *Podocarpus Totara* standing on the edge of the chasm is given by Thomas, who has written perhaps the most comprehensive report of the eruption, although he had not the advantage of having visited the mountain before it took place. He states that forests of large trees grew upon the sides of the Tarawera Mountain, and these of course were wholly wrecked by the eruption. Those on the site of the chasm disappeared altogether. Fortunately the late T. Kirk had ascended the mountain in 1872, and his published papers make it plain that where favourable to plant life the surface of the mountain was clothed with vegetation, though it was scanty and stunted on the highest parts. A dwarf shrubby vegetation was found on the very summit of Tarawera in sheltered places affording cover for a luxuriant growth of mosses and lichens in which the epiphytic *Caladenia bifolia* (northernmost limit), *Thelymitra longifolia* and *Orthoceras Solandri*, occurred. Elsewhere on the summit were *Metrosideros hypericifolia*, *Corokia buddleoides* (southernmost limit), *Coprosma lucida*, *Olearia furfuracea*, *Raoulia Munroi* (northernmost limit), *Dracophyllum strictum*, *D. longifolium* (northernmost limit), *Polypodium serpens*, *Tmesipteris Forsteri*, while near the summit were noticed *Lycopodium volubile* (2800 feet), *Astelia trinervia* (3300 feet), *Cyathodes empetrifolia* and *Gaultheria oppositifolia* (3200 feet).

On the margins of Tarawera Lake he noticed abundant trees of *Metrosideros tomentosa* of large size, *Astelia Cunninghamii*, *Scirpus maritimus*, *Ranunculus accaulis* and *Chenopodium glaucum* var. *ambiguum*¹. At the entrance to the gorge separating Ruawahia from Wahanga, he saw large

¹ Kirk instances other sea-littoral plants such as *Convolvulus soldanella*, *Juncus maritimus*, *Leptocarpus simplex*, *Carex pumila*, *Zoisia pungens*, *Bromus arenaria*, *Poa australis* var. *laevis*, which are found in this thermal district as supporting the theory of the submarine origin of the lowlands of the central portion of the North Island, but when one considers that wild waterfowl, such as shags, black swans and wild duck travel frequently between coast and lakes, and that shags nest in the *Metrosideros tomentosa* trees on the coast, a simpler explanation of the presence of these sea littoral plants in fresh water littoral situations far inland becomes apparent.

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terrestrial specimens of *Metrosideros robusta*, and elsewhere *Panax Colensoi*, the most prominent shrub, forming handsome dwarf bushes sheltering *Hymenophyllum bivalve*, *H. multifidum*, and other ferns; *Danthonia* sp., *Agrostis quadriseta* and *Pittosporum tenuifolium* were also observed. He states that the total number of species collected above 3000 feet did not exceed seventy, and considered that the vegetation of the mountain comprised a remarkably limited number of species.

It would be too much to assume that all vegetation was entirely killed out at the base of the mountain by the eruption of 1886. The dead stumps of large *Metrosideros tomentosa* trees may still be found standing at the lake-side, and species of the family Myrtaceae are so tenacious of life that stumps might have sprouted and produced seed with several feet of mud or scoria round them. Moreover seed might have become uncovered by the rain cutting gulches in the soft mud and sand, and have found the absence of competition from other plants a factor favourable to their growth.

Thus on account of the volcanic origin of Tarawera Mountain and the isolated position of the north-west face, the foot of which, save for one narrow isthmus, is washed by the waters of Lakes Rotomahana and Tarawera, and on account of the eruption of 1886, this area presents peculiar facility for the study of the spread of species on new ground, since only an infinitesimal fraction of the plants could have survived the 1886 eruption¹.

In the spring of 1913 the author twice visited Tarawera, on the first occasion (Sept. 15) ascending to the summit of the range by the broad valley shown in Phot. 3, lying to the north of the landing for Rotomahana Lake, and on the second visit landing on Kanehapa beach and after examining the *Metrosideros* forest proceeding to a point about 1700 feet above sea-level immediately above the beach.

At Kanehapa beach there are two beach levels, the lower consisting of white pumice barren of plant life but mixed with drift wood, the upper beach, a few feet higher, composed of red pumice and sand with patches of *Raoulia australis* dotted about, while growing at the edge of the beach are bushes of *Veronica salicifolia* and *Coriaria ruscifolia*. Scattered about are young plants of a naturalised *Erigeron*. Shrubs of *Myrsine Urvillei*, *Cyathodes acerosa*, *Muehlenbeckia complexa* are near at hand, and *Hydrocotyle asiatica* also occurs. A little to the right of the beach are lava cliffs about 150 feet high which are covered with a growth of young *Metrosideros tomentosa* forest fringed at its margin with *Coriaria ruscifolia* and *Veronica salicifolia*, and containing also the following: *Knightia excelsa*, *Coprosma lucida*, *Leptospermum ericoides*, *Panax arboreum*, *Pittosporum tenuifolium*, *Pittosporum*

¹ A lithographed reproduction, given in Thomas' report, of a photo of Tarawera, seen from the south-west before the eruption, shows dense forest to about one-third of the height above Lake Tarawera.



Phot. 6. Looking at the south end of Tarawera, showing gradual slope to summit avoiding the "mural crown." *Coriaria* shrubberies in middle ground; gravels in foreground with patches of *Raoulia*.



Phot. 7. Beaches at Kanehapa, Lake Tarawera; the dead trees were killed by the eruptions in 1886.

Colensoi, *Geniostoma ligustrifolium*, *Leucopogon fasciculatus*, *Gaultheria antipoda*, *Cyathodes acerosa*, *Haloragis ulata*, *Poa anceps*. Where the forest reaches the shore there are many dead stumps of *Metrosideros tomentosa* which had been killed by the eruption. The illustration gives a very good idea of the vigorous young growth on the lake-side.

In the broad valleys of the lower slopes, where the soil is better, the dominant plant is *Coriaria ruscifolia*, forming pure shrubberies 15 to 20 feet high, the plants having numerous trunks 6 to 8 inches in diameter springing from the ground. On the gravels of temporary watercourses patches of *Raoulia australis* are attempting to form a covering. In the more exposed situations where the soil is poorer and not so moist and the altitude greater the *Coriaria* is replaced wholly or in part by *Leptospermum scoparium* (see Plate V, Phot. 6).

Ascending a deep gully above Kanehapa beach where surface water had cut the beds of ash into a vertical-walled ravine, the following were noticed between lake level (1040 feet) and 1500 feet above sea. Woody shrubs: *Metrosideros tomentosa*, *Weinmannia racemosa*, *Pittosporum tenuifolium*, *Leptospermum scoparium*, *Veronica salicifolia*, *Olearia furfuracea*, *Fuchsia excorticata*, *Melicystus ramiflorus*, *Rubus australis*, *Griselinia littoralis*, *Leucopogon fasciculatus*, *L. Frazeri*, *Gaultheria oppositifolia* (in large masses 6 feet across on the walls of the gorge), *Muehlenbeckia australis*, *M. axillaris*, *Pimelia laevigata*, *Solanum avicularis*, *Coprosma robusta*, *Melicystus ramiflorus*. Herbs: *Angallis arvensis* (naturalised), *Epilobium rotundifolium*, *Dianella intermedia*, *Gahnia* sp., *Cladium Vauthieri*, *Acaena sanguisorbae*. Ferns: *Pteris esculenta*, *P. tremula*, *Lomaria procera*, *Asplenium flaccidum*, *A. falcatum*, *A. lucidum*, *Polypodium Billardieri*, *P. pennigerum*, *P. serpens*, *Hemitelia Smithii*, *Cyathea dealbata*, *Pellaea rotundifolia*.

We now come to scoria flats, supporting a sparse growth, 2 to 6 feet high, of *Coriaria ruscifolia*, *Pteris esculenta*, *Veronica salicifolia*, *Olearia furfuracea*, *Coprosma robusta*, *Weinmannia racemosa*, *Leptospermum scoparium*, while patches of *Pimelia laevigata* a foot or more in height are closely appressed to the pumice gravel.

Finally at 1550 feet open stony slopes are reached where the rise is so gentle as to be hardly perceptible. Here the growth of shrubs is still more scanty. The *Pteris* disappears and the vegetation is *Leptospermum ericoides*, *Coriaria ruscifolia*, *Veronica salicifolia*, *Pimelia* patches, and numerous young plants of the naturalised *Oenothera odorata*, evidently seedlings from last year's old plants. From this point to the "mural crown," vegetation was not inspected, the journey to the summit being made by a more southerly route where by avoiding the "mural crown" and by travelling for a while on the edge of the great chasm the top of the range is more easily approached (Plate V, Phot. 6). On this route in addition to many of those already

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mentioned the following were seen up to 1800 feet. Shrubs: *Aristotelia racemosa*, *Arundo conspicua*. Herbs: *Epilobium nummularifolium*, *Raoulia australis*, *Gnaphalium luteoalbum*, *Wahlenbergia gracilis*, *Thelymitra* sp., *Danthonia semiannularis*, *Raoulia glabra*, *Carex* sp., *Sonchus oleraceus*, *Erechtites scaberula*; naturalised plants of *Hypochaeris radicata*, *Trifolium repens*, *T. pratense*. Ferns: *Pteris esculenta*.

At 1800 feet a few stunted shrubs of *Weinmannia racemosa*, *Gaultheria oppositifolia*, *G. antipoda*, *Leucopogon fasciculatus*, *L. Frazeri*, *Dracophyllum subulatum*, *Muehlenbeckia axillaris*, *Cyathodes empetrifolia*, *Drosera auriculata*, *Metrosideros robusta*, *Griselinia littoralis*, *Dodonea viscosa*, and patches of *Raoulia australis*, together with *Lomaria alpina*, *L. capense*, *Polypodium Billardieri* and *Lycopodium densum*.

On compacted scoria slopes at 3000 feet patches of *Raoulia tenuicaulis* in flower, *R. australis*, *Danthonia semiannularis* and *Hypochaeris* seedlings were the higher plants, while occasionally in a damper cavity than usual a fern would be found, and patches of moss.

On the summit of Ruawahia there is a cap of red scoria on which the only growth at present are patches of silvery *Raoulia australis*.

On account of the Tarawera Mountain Range having been built up by successive outflows of lava, ashes, and mud, and also on account of its isolated position, its flora might be expected to show species which are specially adapted to spreading easily by means of wind and water, and birds, and this we find to be the case. Practically the whole of the plants found on the mountain are those the seed of which is spread in this manner. The species which have succulent edible fruits, and which therefore are spread by means of birds, hold first place, while those which have light seeds or seeds furnished with special structures enabling them to float in the wind and capable of travelling long distances in the air are a good second. And this is true of the plants observed by Kirk in 1872 before the eruption, as well as of those recorded by me in 1913, twenty-seven years afterwards.

Appended are notes on the principal forest trees of the Rotorua district, which should of course be growing on the lower slopes of Tarawera, but owing to their heavy seed are unable to get there.

Kirk records the following as "chief trees of Ngongotaha (a forest-clad mountain 2554 feet high, 7 miles west of Rotorua) and the adjacent hills: *Dacrydium cupressinum* Sol., "Rimu" (nut ovoid, 3 mm.); *Metrosideros robusta* A. Cunn.; *Beilschmidia Tawa* Benth. and Hook. f., "Tawa," constituting 75 per cent. of the millable timber in some parts of the Rotorua district (berry 2.5 cm. long and solitary-seeded); *Knightia excelsa* R. Br., "Rewa-rewa" (pubescent follicles 4 cm. long, tapering into the persistent style, ultimately splitting into two boat-shaped valves containing three or four winged seeds); *Litsea calicaris* Benth. and Hook. f., "Mangeao" (solitary-

seeded berry, 2 cm. long); *Laurelia novae-zealandiae* A. Cunn., "Pukatea" (achenes hairy, narrowing into long plumose styles)—this tree is common in the forests on the west side of Lake Tarawera. Abundant in the forest at the north end of Lake Rotorua, according to Kirk, are the following trees: *Elaeocarpus dentatus* Vahl, "Hinau" (drupe about 12 mm. long, oblong, ovoid, stone rugose, 1-celled, 1-seeded); *Metrosideros robusta* A. Cunn., "Rata" (capsule coriaceous, 3-celled, 3-valved or irregularly dehiscent, seeds densely packed, numerous, linear); *Podocarpus spicatus* R. Br., "Matai" (drupe 8 mm. in diameter); *Podocarpus ferrugineus* D. Don, "Miro" (drupe 2 cm. long); *Knightia excelsa* R. Br.; *Litsea calicaris* Benth. and Hook. Much less frequent, he says, are *Weinmannia racemosa* Linn. f., "Tawhero" (capsule 5 mm. long, 2- to 3-valved, seeds hairy, minute, and numerous)—Don's name for this genus was *Leiospermum*; *Fusanus Cunninghamii* Benth. and Hook. f. (drupe 8 to 12 mm. long); *Ixerba brexioides* A. Cunn. (capsule 2 cm. in diameter, seeds large, oblong, compressed).

In addition to those given by Kirk the following might be mentioned from my own observations: *Carmichaelia* sp., probably *C. juncea* Col., common in many parts of the Rotorua district, leguminous seeds; *Persoonia Toru* A. Cunn., "Toro" (drupe 8 to 12 mm. long, 1- or 2-celled with single seed in each cell), common on Karamea (Rainbow Mountain). The forest near Te Wairoa, the Maori village buried at the time of the eruption, now contains *Laurelia novae-zealandiae* A. Cunn. (this species may require soil conditions which do not occur on Tarawera); while at the Te Ngae forest, about ten miles further away, I noticed *Podocarpus dacrydioides* A. Rich., "Kihahitea" (fruit a black ovoid nut about 4 mm. long); *Carpodetus serratus* Forst. (fruit globose, size of small pea, almost fleshy, indehiscent 3- to 5-celled, seeds numerous, pendulous); *Clematis indivisa* Willd. (achenes with a plumose tail often more than 5 cm. long).

List of Species found on Tarawera Mountain, Western Face, in September, 1913¹

Species	Form of fruit
B. <i>Melicystus ramiflorus</i> Forst.	Small berry.
B. <i>Pittosporum tenuifolium</i> Banks and Sol.	Capsule woody and seeds sticky.
B. <i>Aristotelia racemosa</i> Hook. f.	Berry size of a pea.
W. <i>Dodonaea viscosa</i> Jacq., above 1400 feet	Membranous compressed capsule, very broadly 2- to 3-winged. Wings membranous.

¹ A letter "B" prefixed to the name of the species denotes the probability of its being spread by birds and "W" by wind, while "?" before a name denotes that the method of dispersal is doubtful, but possibly by wild animals (rabbits or hares) or by water (floated across) or by water fowl.

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Species	Form of Fruit
B. <i>Coriaria ruscifolia</i> Linn., above 1400 feet	Crustaceous achenes invested by juicy petals.
B. <i>Rubus australis</i> Forst.	Many succulent 1-seeded drupes crowded upon a dry receptacle.
? <i>Acaena sanguisorbae</i> Vahl.	Achenes attached to fruiting calyx of four barbed bristles.
? <i>Weinmannia racemosa</i> Linn. f., above 1400 feet	Capsule containing small hairy seeds.
W. <i>Drosera auriculata</i> Backhh., above 1400 feet	Seeds minute.
W. <i>Haloragis alata</i> Jacq.	Small, dry, 2- to 4-seeded nut, 2-3 mm. long with four ribs dilated into wings.
W. <i>Leptospermum scoparium</i> Forst., above 1400 feet	Woody or coriaceous capsule, containing numerous linear seeds. Generic name means "slender seed."
W. <i>Metrosideros flavida</i> Smith, above 1400 feet	Coriaceous or woody capsule.
W. ,, <i>tomentosa</i> A. Rich.	Seeds numerous, linear.
W. <i>Epilobium rotundifolium</i> Forst.	Capsule 4-angled, seeds numerous, furnished with a tuft of long hair at the summit.
W. ,, <i>nummularifolium</i> R. Cunn. }	
W. ,, <i>melanocaulon</i> Hook. }	
B. <i>Fuchsia excorticata</i> Linn. f.	Fleshy, many-seeded berry.
? <i>Hydrocotyle asiatica</i> Linn.	Two dry, indehiscent cohering carpels.
B. <i>Panax arboreum</i> Forst.	2- to 4-celled succulent exocarp.
B. <i>Griselinia littoralis</i> Raoul, above 1400 feet	Small 1-seeded berry.
B. <i>Coprosma lucida</i> , Forst.	2-seeded fleshy drupe.
B. ,, <i>robusta</i> Raoul, above 1400 feet	2-seeded fleshy drupe.
W. <i>Olearia furfuracea</i> Hook. f., above 1400 feet	Composite. Achenes small, with pappus hairs.
W. <i>Gnaphalium luteo-album</i> Linn.	Achenes minutely papillose.
W. <i>Raoulia australis</i> Hook. f. var. <i>lutescens</i>	Achenes with numerous extremely slender pappus hairs.
W. ,, <i>tenuicaulis</i> Hook. f., above 1400 feet	Achenes with copious pappus hairs.
W. ,, <i>glabra</i> Hook. f.	Puberulous achenes.
W. <i>Erechtites scaberula</i> Hook. f.	Achenes with many series of copious soft slender pappus hairs.
W. <i>Sonchus oleraceus</i> Linn.	Achenes with many series of copious soft slender pappus hairs.
? <i>Wahlenbergia gracilis</i> A. D'C.	Capsules 2- to 5-celled, seeds numerous, small, compressed.
B. <i>Gaultheria antipoda</i> Forst., above 1400 feet	Capsule included in large and succulent calyx and lobes. Seeds minute.
W. ,, <i>oppositifolia</i> Hook. f., above 1400 feet	Capsule dry, seeds minute.
B. <i>Cyathodes acerosa</i> R. Br.	A baccate succulent drupe.
B. ,, <i>empetrifolia</i> Hook. f., above 1400 feet	3- to 5- celled small drupe.
B. <i>Leucopogon fasciculatus</i> A. Rich., above 1400 feet	Small baccate drupe.
B. ,, <i>Frazeri</i> A. Cunn., above 1400 feet	Small baccate drupe.

Species	Form of Fruit
W. <i>Dracophyllum subulatum</i> Hook. f.	5-celled capsule with numerous seeds.
B. <i>Myrsine Urvillei</i> A. D'C.	Fruit small, globose, drupaceous, dry or fleshy.
? <i>Geniostoma ligustrifolium</i> A. Cunn.	Capsule splitting into two boat-shaped valves. Seeds numerous.
B. <i>Solanum aviculare</i> Forst.	Large many-seeded berry.
W. <i>Veronica salicifolia</i> Forst., above 1400 ft.	Capsule.
B. <i>Muehlenbeckia complexa</i> Meissn.	Small nut enclosed in a succulent perianth.
B. „ <i>axillaris</i> Walp., above 1400 feet	Small nut enclosed in a succulent perianth.
? <i>Knightia excelsa</i> R. Br.	Coriaceous 1-celled, 4-seeded follicles, 4 cm. long, tapering into a persistent style, ultimately splitting into two boat-shaped valves. Seeds winged at the top.
B. <i>Pimelia laevigata</i> Gaertn., above 1400 feet	Fruit usually baccate.
W. <i>Thelymitra longifolia</i> Forst.	Orchid. Seeds very minute.
B. <i>Dianella intermedia</i> Endl.	Berry.
? <i>Juncus</i> sp.	Capsule, small seeded.
? <i>Gahnia</i> sp.	Hard and bony nut.
? „ <i>gaudichaudiana</i> Steud., above 1400 feet	Nut small.
? <i>Carex</i> sp.	Nut.
W. <i>Danthonia semiannularis</i> R. Br., above 1400 feet	Caryopsis.
W. <i>Arundo conspicua</i> Forst.	„
W. <i>Poa anceps</i> Forst.	„
W. <i>Cyathea dealbata</i> Swartz.	Spores.
W. <i>Hemitelia Smithii</i> Hook.	„
W. <i>Pellaea rotundifolia</i> Hook.	„
W. <i>Pteris aquilina</i> Linn. var. <i>esculenta</i> , above 1400 feet	„
W. „ <i>tremula</i> R. Br.	„
W. <i>Lomaria</i> sp., above 1400 feet	„
W. „ <i>alpina</i> Spreng., above 1400 feet	„
W. „ <i>capensis</i> Willd., above 1400 feet	„
W. <i>Asplenium falcatum</i> Lam.	„
W. „ <i>lucidum</i> Forst.	„
W. „ <i>flaccidum</i> Forst.	„
W. <i>Polypodium pennigerum</i> Forst.	„
W. „ <i>serpens</i> Forst.	„
W. „ <i>Billardieri</i> , R. Br.	„

Naturalised plants

<i>Trifolium repens</i> Linn.	Possibly introduced by rabbits.
W. <i>Erigeron canadensis</i> Linn.	
W. <i>Hypochaeris radicata</i> Linn.	
W. <i>Anagallis arvensis</i> Linn.	
W. <i>Oenothera odorata</i>	

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THE SALT MARSHES OF THE DOVEY ESTUARY

BY R. H. YAPP, D. JOHNS AND O. T. JONES.

PART I. INTRODUCTORY

(With three Figures in the Text)

(a) THE GEOLOGICAL HISTORY OF THE DOVEY ESTUARY AND THE ADJOINING FLATS. BY O. T. JONES

The hills which bound the Dovey Estuary are composed of slaty rocks with some grits and mudstones; they belong to the higher part of the Ordovician and the lower part of the Silurian system¹.

The rocks are grey, dark-blue or occasionally almost black; the latter especially contain finely-divided iron pyrite which on weathering appears as hydrated oxide of iron. All the rocks are deficient in lime; only occasionally do nodules of impure limestone occur.

The strata are sharply folded and faulted; their strike is approximately N.N.E.-S.S.W. Some of the faults carry ores of lead, zinc or copper and these are sometimes associated with some calcite. With these exceptions none of the streams draining into the estuary have access to any considerable sources of lime.

During the glacial period the valley and estuary were occupied by ice which came down from the Ordovician volcanic range of Cader Idris and Aran Mawddwy. The boulder clay derived from the attrition of the more basic rocks (andesites) of that range might contain small amounts of lime, but it cannot be significant. The level tract (named in this paper the Dovey Flats) is interrupted here and there by rounded island-like masses of solid rock, whence the name Ynys (Engl. = island) applied to them; their slopes pass beneath the surrounding deposits. The nature of those deposits is unknown with the exception of a limited thickness of their upper part which is exposed in the banks of water courses and in peat cuttings. Such sections indicate that in some parts of the area a few feet of peat occur beneath the surface while in other parts a thickness of several feet of tough blue clay is exposed. The clay areas appear to mark the former courses across the

¹ Jones, O. T. and Fugh, W. J., *Quart. Journ. Geol. Soc.*, **71**, 1915, p. 343. (Published 1916.)

tract of the Einion, Clettwr, Leri and other streams. Owing probably to the wandering of the stream channels the beds of clay towards the margin of the areas alternate with peaty beds; the former diminish in thickness away from the old stream courses and finally disappear.

The western boundary of the Flats is formed by a storm-beach which extends northwards from the cliffs near Borth for two or three miles; in the lee of the storm-beach a narrow belt of blown sand encroaches on the Flats and at the northern end of the beach extends for some distance beyond it towards the estuary (see map, Fig. 3)¹.

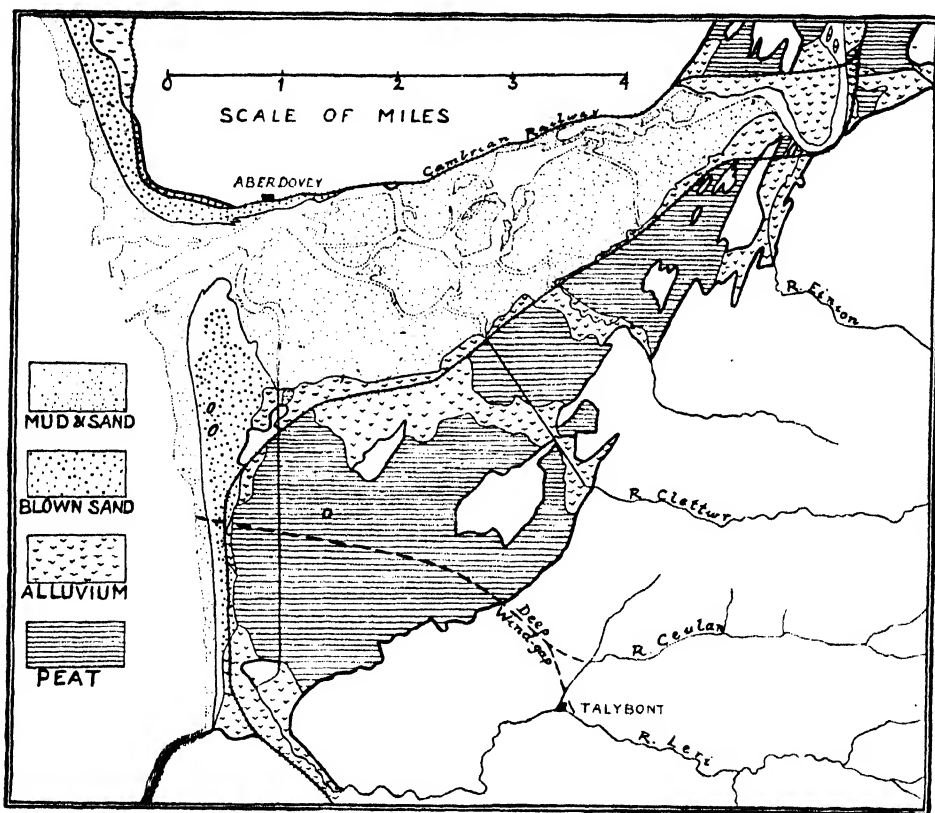


FIG. 3. Map of the surface geology of the Dovey Flats. The areas left white on the Flats represent outcrops of rock. --- Probable pre-glacial course of the River Leri. The thick line marks the boundary of the post-glacial deposits.

On the foreshore a submerged forest is exposed at low water. It rests upon tough blue clay similar in appearance to that which forms certain areas within the Flats. There is reason to suppose that the level of the forest at that point is at least as low as the bed of the Leri in its present artificial course across the Flats, for the natural channel of that stream in post-glacial times was close to the storm-beach, and probably always occupied

¹ The deposits of the Dovey Flats were surveyed, under my direction, by Mr R. U. Sayce and Mr W. J. Pugh, as part of a complete geological survey of the Aberystwyth district.

that position relative to the beach. In the course of the migration of the storm-beach landwards, which has obviously occurred since the forest was in existence, the channel of the Leri must have passed over the spot where the forest now stands without destroying it. The blue clay under the forest is therefore the lowest deposit that is exposed within the area, and there is as yet no evidence of the nature or thickness of the deposits that underlie it. The blue clay itself is probably an estuarine or river silt, and is not boulder clay.

It is known that in several places along the line of the Cambrian Railway the solid rock is more than 80 or 90 feet below the level of the Dovey Flats, while near Dovey Junction the rock-floor lies more than 150 feet below sea-level¹.

The geological history of the estuaries on the west coast of Britain is still imperfectly known; but it is assumed that the history of the Dovey Estuary was in the main similar to that of other estuaries north and south.

At some time in the Tertiary period the area bordering the present coast had been reduced by denudation to a surface of low relief. A subsequent uplift raised it some hundreds of feet above sea-level and in this uplifted plain or plateau the present rivers incised steep-sided rather narrow valleys, the mouths of which were at grade with the new level of the sea. Erosion during the glacial period modified slightly the form of the valleys, especially those which lay in the direction of ice-movement. After the retreat of the ice the floor of the valleys and probably also a considerable area of Cardigan Bay was covered with boulder-clay.

Marine erosion has not yet removed this deposit from all parts of the coast and the pre-glacial cliffs are still in places some distance inland.

Whether the rock-floor of the valley was excavated to its present great depth by glacial erosion or by the river when the land stood at a higher level than at present remains to be proved.

That subsidence of the Dovey area has occurred is indicated by the submerged forest at Borth, but in some estuaries on the west, south and east coasts of Britain there are two or more submerged forests and the deepest of these indicates subsidence of those tracts of at least 70 feet since the growth of their forest vegetation².

Again in the Barmouth estuary, some 12 or 14 miles north of the Dovey, a peat bed was proved in sinking the foundations for the railway bridge at a depth of 40 feet below the level of low water, or about 55 feet below the level of high water at ordinary spring tides³.

¹ For the information contained in this sentence I am indebted to Mr Abraham Williams, Aberdovey.

² **Reld, Clement**, "Submerged Forests."

³ **Codrington, T.**, *Quart. Journ. Geol. Soc.*, **54**, 1898, p. 251, and reference.

Near Amroth, north of Tenby¹, and between Porlock and Minehead², flint-flakes, and chips assigned to the Neolithic period have been found in submerged forests similar to the one at Borth, while, in one of the upper peat beds passed through during the construction of the Barry Docks³, a bone needle and a portion of a polished stone celt (Neolithic) were found at a depth of about 5 feet below Ordnance Datum or nearly 25 feet below the level of high water of ordinary spring tides. It is clear therefore that the submergence of those areas has occurred after or during Neolithic times.

Clement Reid considers, moreover, that "the stratigraphical relations seem to indicate that all these deposits are of Neolithic age and later than the Palaeolithic terraces." If this view is confirmed it is clear that a considerable interval of time separates the close of the glacial period and the beginning of the movement of subsidence. By analogy with other estuaries the submergence of the Borth forest may be regarded as the last phase of that movement of depression which carried the earlier forest beds to such great depths below the present sea-level⁴.

It has been suggested that submerged forests do not necessarily imply a depression of the land but may be due to local subsidence. In support of this it may be pointed out that peat beds which rest partly upon solid rock and partly upon soft deposits sag slightly over the latter and are in general thicker, thus proving an unequal subsidence of their foundation⁵.

To account for the local subsidence, compression and packing of the underlying deposits have been invoked, but Shone considers that in many cases it is due to the subterranean erosion or removal of sand and silt by percolating waters.

As Reid points out, however, these explanations cannot account for the deeper submerged forests which in some cases rest upon solid rock.

It may or may not be significant that the Borth submerged forest is now preserved only in that region where the physiographical relations of the tract indicate the existence of a great thickness of deposits, for the boggy peat moor and the area east and west of it probably overlies the pre-glacial valley of the Leri, which is now deeply submerged and filled with glacial and other deposits (compare Figs. 3 and 4). The Leri in pre-glacial times

¹ Leach, A. L., "Archæologia Cambrensis," 1913, p. 391.

² Dawkins, W. Boyd, *Quart. Journ. Geol. Soc.*, 39, 1883, p. 611 (Discussion).

³ Strahan, A., *Quart. Journ. Geol. Soc.*, 52, 1896, p. 474.

⁴ According to a Welsh legend Cardigan Bay was once occupied by an extensive lowland tract (known as Cantref y Gwaelod or the Lowland Hundred), which was protected from inundations of the sea by an embankment. Neglect on the part of its custodian to keep the embankment in order, caused the inundation and disappearance of the tract during a great storm. If the last depression occurred in or after Neolithic times, it is probable that the ancestors of the present inhabitants of Wales already lived in the country, and the legend may therefore rest upon a foundation of fact. There are, however, other possible explanations of the legend.

⁵ Shone, W., *Quart. Journ. Geol. Soc.*, 48, 1892, p. 96.

entered the Dovey area through the deep gap north-west of Talybont and thence probably flowed parallel to, but at some distance south of, the series of "islands" between Tre-Taliesin and Ynys-las (Figs. 3, 4).

On the assumption that part if not most of the subsidence that has affected the coast of Cardigan Bay occurred in post-glacial times, we may attempt briefly to outline the events to which are due the present estuary of the Dovey and the adjoining Flats.

At the close of the glacial period the Dovey valley and an unknown area of Cardigan Bay were occupied by a stiff blue clay containing abundant boulders derived mainly from more northerly localities. The surface of the deposit was uneven, with shallow pools here and there, while at the seaward margin low mounds of boulder clay alternated with irregular embayments into which the sea penetrated. Soon, however, marine erosion developed low cliffs in the soft glacial deposits, the boulders from which accumulated at the foot of the cliffs. Owing to the tidal currents and the prevalence of south-westerly winds material drifts northward along this part of the coast; for this reason a storm-beach grew across the mouth of the embayments or other low-lying tract, the boulders being supplied from the south by the waste of the cliffs. The embayments were therefore cut off from direct communication with the sea and became brackish or even fresh-water pools (*étangs*). The larger rivers, Dovey, Mawddach, etc., flowed across the glacial deposit carving their valleys in it so as to grade with the sea-level. It is probable that tidal scour widened the lower end of the larger valleys and kept them from being blocked by the growth of a storm-beach across their mouths. Estuaries came therefore into existence at an early stage, but their sites lay farther out in Cardigan Bay than at present.

Smaller streams that attempted to reach the sea across the boulder-clay tract were barred by a storm-beach and forced to flow behind it, either to break through at the north side of their valleys, or to percolate through the barrier. The main channel of the larger rivers hugged the northern shore of the estuary, where there was more vigorous undercutting than on the opposite shore (see Fig. 3).

North of the estuary, cliffs of boulder clay extended continuously except where a storm-beach crossed a low-lying marshy tract, or enclosed a shallow lagoon or *étang*.

South of the estuary a strip of storm-beach and probably some blown sand intervened between it and the nearest boulder-clay cliffs.

Conditions similar to these prevail at various points of the coast of Cardigan Bay at the present day.

If no subsidence occurred, erosion of the boulder-clay cliffs would continue steadily; the storm-beaches would be pushed landward across low-lying tracts and river mouths; and the head of the estuaries would advance inland

until ultimately all the glacial deposits had been removed from Cardigan Bay, and the pre-glacial shore line was regained. The appearance of the tract at any stage would not be markedly unlike that of those portions of it that remain at the present day.

The results of subsidence would depend upon (1) the relative rates of depression and sedimentation, and (2) the contours of the submerged surface, i.e. of the valley floor and its slopes of rock and boulder clay. If the subsidence began at a considerable interval after the glacial period, the valley floor above the head of the estuary would be a wide, gently-sloping, alluvial plain, perhaps bounded by some river terraces. If it occurred immediately after the glacial period, the valley would be more irregular and of immature character.

(1) If we assume that the subsidence took place at such a rate that deposition of river-borne and marine sediments could keep pace with it, no extensive drowned area (the site of future marshes or bogs) could occur at any stage of the movement. Changes would begin to be felt at the head of the estuary, where tidal scour would remove parts of the alluvial plain previously beyond the reach of tidal action. There would follow also a tendency to more frequent flooding of these plains, but as the supply of sediment was (according to the assumption) sufficient, this would result in the flooded areas being raised *pari passu* by deposition over their surface. Except for the gradual migration of the head of the estuary, and of the storm-beach at its mouth, and also of the boulder-clay cliffs north and south, the appearance of the tract would remain much the same throughout, and such changes, ultimately involving the submergence of the valley floor to 50 or 100 feet, might proceed without attracting particular attention.

If, on the other hand, subsidence outstripped sedimentation it follows that the alluvial plains above the head of the estuary would pass under the sea and a considerable area might thus be submerged. It would depend on the form of the valley before subsidence began, and on the amount of movement, how the subsequent filling up of the submerged tract would be accomplished; but whatever those conditions, sedimentation would ultimately convert the region into dry land, or more probably dry land would alternate with shallow-water areas which would pass progressively from salt-water pools through brackish-water pools to fresh-water pools and marshes. The evidence of marine occupation of the area would be furnished solely by the nature of the sediments; when the drowned areas had become sufficiently shallow to permit of extensive growth around their margins it is probable that they would be beyond the reach of any except occasional incursions of salt water. It appears therefore that only relatively rapid subsidence is adequate to produce the conditions under which the vegetation of the Borth submerged forest grew.

This conclusion agrees also with what is known of the succession in other estuaries, for the upper submerged forests are overlain by blue clay containing shells of the estuarine bivalve *Scrobicularia piperata* (these are often found with the valves attached in the position of growth). Where more than one forest-bed occurs, it is clear that marsh conditions have given way to estuarine conditions until sedimentation so neutralized the effect of the subsidence as to allow marsh conditions to recur¹.

The known history of other estuaries suggests again that the downward movement has not been continuous but spasmodic (see Sollas, p. 623); periods of depression alternated with pauses during which sedimentation and the growth of vegetation filled up the depressed area. Since the growth of the Borth submerged forest, a further depression has carried the forest beneath sea-level. This drowned the lower end of the valley; sedimentation followed, quickly in some areas, more slowly in others; the present peat-moor may represent one of the latter areas where the levelling up of the tract has been completed by the growth of the bog vegetation. It may be suggested therefore that the depth of peat is nowhere great (probably not greater than the amount of subsidence indicated by the submerged forest), and that it rests partly upon river-borne or marine silt and partly upon such areas of boulder-clay or rock as had escaped submergence at the time when the forest on the foreshore was depressed.

The agreement between the probable consequences of a relatively rapid movement and the physiographic conditions of the area may be regarded as confirming that hypothesis; direct evidence can only be obtained by having a series of borings or excavations made to determine the nature and succession of the deposits underlying the Dovey Flats.

It is interesting to observe in this connection that Clement Reid has arrived, by a different line of reasoning, at the conclusion that the whole of the changes resulting in a depression of perhaps more than 80 feet possibly occurred in less than 1500 years, which in a geological sense may be regarded as a rapid movement.

(2) It may be of interest to consider how the condition of the lower end of the valley at any stage depended upon the form of the valley floor prior to submergence, and upon the amount of movement. Two cases may be considered. (a) If the height of the boulder-clay tract in Cardigan Bay above the level of the estuary was small in comparison with the submergence, a large area adjoining the valley would disappear, and the coast-line would migrate some distance inland. Owing to the rise of the valley floor inland the depth of water opposite the new position of the shore line to the north and south would not be great. Cliff cutting would start at the new level and on

¹ *Mem. Geol. Survey: South Wales Coalfield*, pt. viii, 1907, p. 143; **Reid, Clement**, "Submerged Forests," p. 51; **Sollas**, *Quart. Journ. Geol. Soc.*, **39**, 1883, p. 611.

account of the relatively small depth of water in line with the coast a storm-beach would gradually extend northwards thus defining sharply the lower end of the drowned valley. The submerged area lying within the storm-beach and the slopes of the valley would partly silt up with fresh-water and marine silt—deposition being most rapid at the head of the area and in the shallow water, especially along its southern margin, but proceeding also in patches elsewhere. Ultimately the stream-course of the Dovey and of its tributaries would be defined by low banks or levées and the intervening areas would pass successively from salt-water to fresh-water pools and finally become marshes or peat bogs. The farther a place happened to be from stream-channels the more likely it would be to escape sedimentation. The wandering stream-courses would therefore be indicated on the surface by areas of fine silty clay. (b) If the boulder-clay tract was too high to be submerged the drowned area would be confined to the comparatively narrow floor of the valley, while the cliffs would diminish in height by the amount of subsidence. Wave erosion would commence at the new level, but in the early stages the depth of water in line with the cliffs would be too great to allow of the formation of a storm-beach; accordingly the drowned area would remain freely open to the sea. Tidal scour with cliff cutting would occur along the margins of the valley while silting would at first be confined mainly to its head and would be due therefore to river-borne sediment—the process being analogous to the formation of a delta in a lake. The valley above the drowned area would be aggraded in order to maintain the necessary gradient for the river. This state of affairs is comparable to that which is found at the lower end of some Devon or Cornish valleys at the present day.

The formation of a storm-beach across the mouth of the estuary would only commence after silting of the lower end of the valley by the formation of sandbanks had proceeded. Before this the boulders removed from the cliffs would either accumulate at the cliff foot and thus retard the erosion or they would be drawn back by the force of the waves into deeper water. It is probable that the later stages of the filling of the valley by silt and vegetable growth would proceed as in the case previously considered.

On the whole it seems that the conditions indicated in the first case are those most likely to have occurred in the Dovey area.

(b) THE DISTRIBUTION OF VEGETATION ON THE FLATS OF THE
DOVEY VALLEY. BY R. H. YAPP

The north-western extremity of Cardiganshire is occupied by the Flats of the Dovey (or Dyfi) valley, a roughly triangular area of low-lying, marshy land, about 5000 acres in extent, stretching from Borth to Glandovey. The geological history of this area has been dealt with above by Professor

O. T. Jones, while the present brief sketch of its vegetation is intended to direct the attention of botanists to the interesting character of the district; to indicate a few of the many ecological problems which await solution; and finally to show the topographical relations between the salt marshes and other types of vegetation.

The present distribution of vegetation on the Dovey Flats is seen in Fig. 4¹. Cultivated and ordinary pasture-land, as well as all land above the

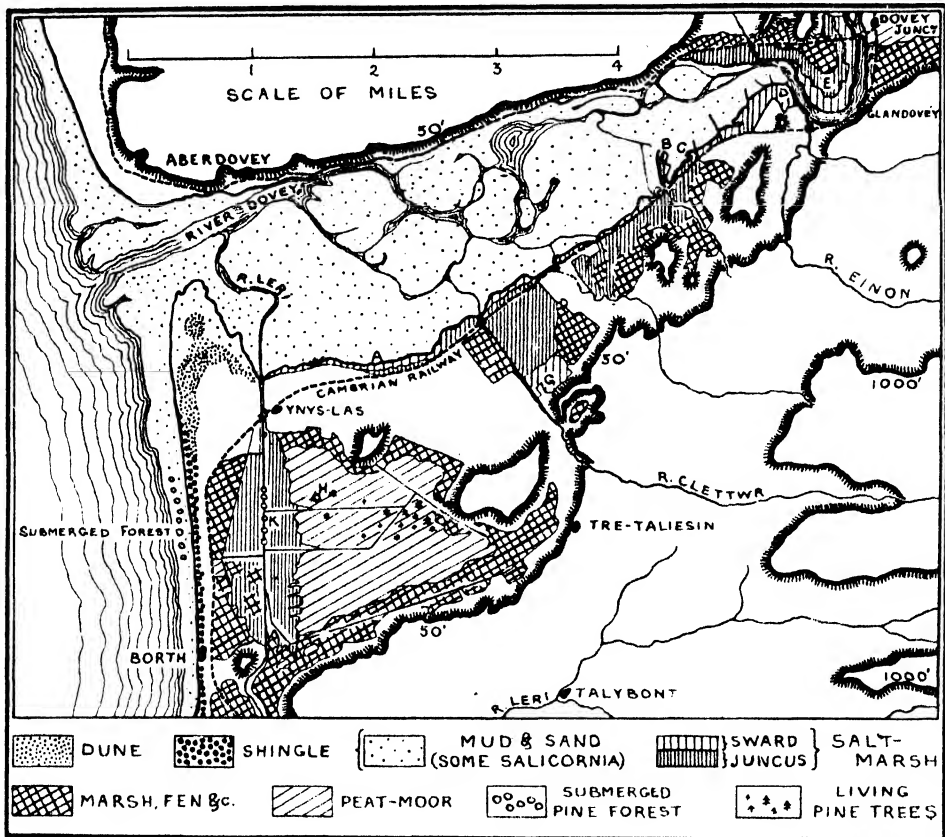


FIG. 4. Map showing present distribution of vegetation on the Dovey Flats. The thick lines, shaded on one side, indicate the 50-foot and 1000-foot contours.

50-foot contour, is left blank; it may therefore be readily seen that the greater part of the Flats is covered by more or less natural vegetation.

From the cliffs to the south of Borth, northwards along the coast, stretches a fringing shingle-beach, some two to three miles in length, and composed

¹ In the main I am responsible for the map forming Fig. 4, but I wish to acknowledge the valuable help of Mr R. G. Stapledon, who supplied a good many details with regard to the vegetation of parts I was unable to visit. Mr Stapledon is engaged in the preparation of a primary survey (now nearing completion) of the vegetation of the whole of the Aberystwyth district.

for the most part of coarse shingle. As the estuary is approached, the shingle gives place to a series of sand-dunes. The greater part, however, of the low-lying and ill-drained Flats is occupied by various types of vegetation characteristic of soils with a high water-content. In the distribution of these types the influence of edaphic factors is clearly and unmistakably seen. Thus we have (1) an extensive central area of wet, lowland peat-moor or bog, developed on the widest portion of the Flats, away from the influence of the streams which intersect them in other parts (Fig. 4). Here the water is stagnant and there is comparative freedom from mineral salts in general, and calcium carbonate in particular¹. (2) Surrounding the moor, where the peat is thinning out, and an abundance of salts is ensured by river alluvium or by rain-wash from the uplands, is a heterogeneous fringe composed of various marsh, fen or transitional associations. (3) Finally, the tidal waters, both of the Dovey and its tributaries, are usually lined by salt marshes.

The maritime formations need not be dealt with here, but a few notes on the moorland vegetation, with its marginal associations, may be of interest.

(a) **The Moorland.** Amongst the most abundant species are the following: *Sphagnum* spp., *Eriophorum angustifolium*, *E. vaginatum*, *Erica Tetralix*, *Scirpus caespitosus*, *Calluna vulgaris* and *Carex panicea*. The distribution of the associations characterized by these dominant species—**Sphagnetum**, **Callunetum**, etc.—is here, as elsewhere, determined largely by water-content, and hence by minor inequalities of level. Thus in the wetter parts, *Sphagnum* is usually dominant, while the drier, elevated ridges or mounds of peat are invariably occupied by **Callunetum**. In a few spots *Cladina sylvatica* is so abundant as to be practically dominant, while *Myrica Gale* is everywhere plentiful, or indeed often dominant, especially in the most central parts of the moor, where it is associated with a very restricted flora.

Abundant, locally abundant, or frequent species include *Andromeda polifolia*, *Rhynchospora alba*, *R. fusca*, *Narthecium ossifragum*, *Hypericum elodes*, *Eleocharis multicaulis*, *Drosera rotundifolia*, *D. longifolia* and *D. anglica*. Two other carnivorous plants also occur, i.e. *Pinguicula vulgaris* and, in the water in old peat cuttings, *Utricularia* (probably *U. intermedia*).

Occasional species are *Menyanthes trifoliata*, *Oxycoccus quadripetalus* and *Osmunda regalis*.

This list is of course far from being exhaustive.

A prominent feature of the moor is a small, wooded outcrop of rock which rises like an island a few feet above the general level of the bog. It is known locally as Llwyn-y-garreg (H, Fig. 4, also Fig. 5). The summit of this "island," which is covered by a very shallow soil, devoid of peat, is occupied

¹ See introduction by Prof. Jones, p. 27.

by an ordinary land flora, such plants as *Scilla nonscripta*, *Teucrium Scorodonia*, *Crataegus*, *Quercus* and many others being found. Descending from the actual rock-outcrop, the following associations are met with at successively lower levels: (1) A well-marked **Betuletum tomentosae**, on fairly dry, shallow peat. The taller birches stand high above the general level of the bog, and exhibit a characteristic wind-swept form (Fig. 5). Mixed with the

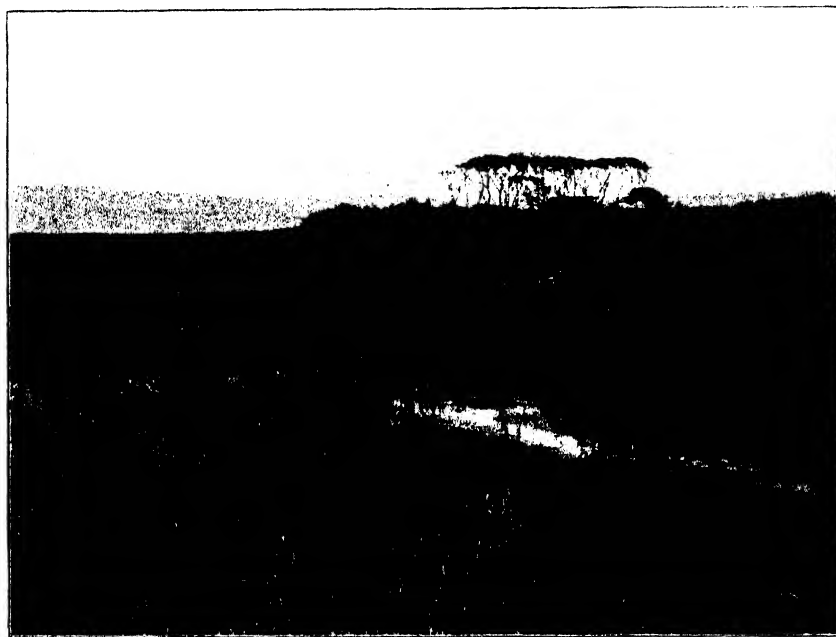


FIG. 5. Llyn-y-garreg from the north-west. Birches form the most prominent feature of the "island." The older trees occupy the centre of the **Betuletum tomentosae**, while surrounding them is a dense belt of younger trees mixed with *Pteris*, showing that the association is extending radially. The moorland vegetation seen consists mainly of *Erica Tetralix*, *Eriophorum vaginatum*, and *Myrica*, with some *Calluna* and *Cladina sylvatica*. In the foreground is a drainage depression showing bare peat, colonized only by *Rhynchospora alba* (in the immediate foreground) and *Eriophorum angustifolium* (in the damper parts). October, 1910.

birches are a few individuals of *Pyrus Aucuparia*. The dominant undergrowth plants are *Pteris aquilina* and a luxuriant form of *Molinia caerulea*. (2) **Callunetum vulgaris**. In this association *Myrica Gale* and a more stunted form of *Molinia caerulea* are abundant, and dwarf *Pteris* and young birches frequent. (3) **Eriophoretum vaginati**. In this *Erica Tetralix* is abundant, while stunted *Calluna* and other plants occur¹.

The summit of Llyn-y-garreg is only some five feet above the general level of the moor. Thus the marked radial zonation in the vegetation around

¹ Cf. the succession on estuarine moors described by Rankin, in Tansley, "Types of British Vegetation" (Camb. Univ. Press, 1911), p. 250.

Llwyn-y-garreg appears to demonstrate the effect of slight differences of level as clearly as does the similar zonation exhibited in the salt marshes to be described in the main paper¹.

The summits of ridges and mounds of somewhat slighter elevation than Llwyn-y-garreg may be covered with peat. They are frequently clothed with *Pteris* only, or, especially when occurring along the western boundary of the moor, with a mixture of *Pteris* and *Ulex europaeus*.

Another noteworthy feature of the moor is the abundance of shallow drainage depressions in the peat. These have no outlets and are for the most part devoid of vegetation. Only certain species, and these usually not very abundant in individuals, occur in them (Fig. 5). The wetter depressions, in which water frequently stands for considerable periods, are usually fringed by *Sphagnum* and have a somewhat more varied flora than the drier, more easily drained hollows. The following lists comprise the chief plants occurring in these drainage depressions:

Wetter depressions			Drier depressions		
<i>Sphagnum</i> spp.	}	... d	<i>Rhynchospora alba</i>	...	d
<i>Rhynchospora fusca</i>			<i>Drosera longifolia</i>	...	a
<i>Eriophorum angustifolium</i>		a	<i>D. rotundifolia</i>	...	f
<i>Rhynchospora alba</i>	...	a	<i>D. anglica</i>	...	o
<i>Drosera rotundifolia</i>	...	f			
<i>Eleocharis multicaulis</i>	...	f			
<i>Menyanthes trifoliata</i>	...	o			

The association of *Rhynchospora alba* and *Drosera* spp. (often the only phanerogamic inhabitants of the drier peat-hollows) is a remarkable one. Mr Stapledon, who has examined many of these hollows on the Dovey moor, tells me he has seen nothing like it on the upland moors of Cardiganshire.

In many respects these curious depressions seem to afford a remarkable parallel to the salt marsh "pans" to be described in the main paper. Apparently they are persistent, and so form a permanent feature of the bog. The method of formation and subsequent history of these stagnant hollows would well repay detailed study.

(b) **The Marginal Associations.** Surrounding the moorland is a belt (indicated by cross-hatching and designated "marsh, fen, etc." in Fig. 4) which includes a variety of plant-associations. In some parts this marginal belt consists of pure ***Molinietum caeruleae***, in others of a mixed marsh association, or here and there something intermediate between marsh and fen. It also includes (especially to the west of the River Leri) considerable

¹ Water-content is undoubtedly an important factor, but the possible influence of mineral salts, due to the proximity of the rock-outcrop, must not be lost sight of. The case of *Molinia* is discussed below.

areas of rough, marshy pasture, with *Juncus conglomeratus* frequent to dominant, and an abundance of Carices, e.g. *Carex panicea*, *C. flava*, *C. Goodenowii* and *C. vulpina*¹.

The distribution of *Molinia caerulea* on the moor and in the marginal belt calls for special notice. *Molinia* is absent from the stagnant central portions of the moor, but is extremely common in the marginal associations². Near Tre-Taliesin on the east (Fig. 4), we find an almost pure **Molinietum**, with large, luxuriant tussocks. On the west, the transitional zone between the moor and the salt marsh fringing the River Leri (too narrow to be indicated in Fig. 4) is characterized by an abundance of *Molinia*, mixed with *Calluna*, *Juncus maritimus*, etc. Indeed, throughout the area, *Molinia* associates freely with the **Juncetum maritimi** (see later) along its landward margin, which is liable only to occasional inundations by the sea. Again, *Molinia* is both plentiful and luxuriant in the immediate neighbourhood of rock-outcrops, such as Llwyn-y-garreg, but becomes stunted and ultimately disappears at some distance from the exposed rock. Finally, the drains which intersect the bog at various points, and are connected with the present tidal channel of the Leri, are usually fringed by *Molinia*.

Several authors³ have drawn attention to the interesting problems presented by *Molinia caerulea*, while Jefferies⁴ has made an excellent autecological study dealing with the distribution of this species on the Yorkshire moors.

Jefferies concludes that "the distribution of *Molinia* depends primarily upon an abundant supply of relatively fresh water—whenever stagnation becomes pronounced, so that the water is badly aerated and excessively acid, *Molinia* tends to degenerate." Now, as far as mere field observations go, the distribution of *Molinia* on the Dovey Flats (cf. Fig. 4) would seem to suggest that, for this plant, mineral salts may play a part at least as important as the factors of aeration and acidity. This much appears certain, that *Molinia* occurs in abundance only in those parts where, on *a priori* grounds, we may assume the substratum to be moderately rich in mineral salts. Thus, on the Dovey Flats, *Molinia* abounds (1) in marginal associations influenced either by rain-wash from the uplands, or by river alluvium, (2) in the transitional zone between moor (or other associations) and salt marsh, or on the edges of drains connected with tidal waters, and (3) in the immediate neighbourhood of small rock-outcrops, where there can be no question of any considerable movement of water.

¹ Mr Stapledon says this species is not met with on similar pastures elsewhere in the Aberystwyth district.

² *Molinietum* as a marginal association of moorland is also described by Smith, R. (Botanical Survey of Scotland: North Perthshire District, Bartholomew, 1900, p. 28), Moss and Rankin (Tansley, *l.c.*, pp. 136, 251 and 262).

³ Tansley, *l.c.*, p. 252; also Moss, "Vegetation of the Peak District," 1913, p. 114.

⁴ Jefferies, "Ecology of the Purple Heath Grass (*Molinia caerulea*)." This JOURNAL, 3, 1915.

To sum up, the **Molinietum** appears to be, as suggested by Tansley¹, "intermediate between the fen formation and the moor formation." It is a characteristic association of fenland, the peat of which is relatively rich in mineral salts. Where, however, it occurs on moors, it is either as a marginal association, or in flushes or other spots presumably richer in salts than is the peat underlying the more typical moorland associations. Thus the observed preference of *Molinia* for moving rather than stagnant water² may possibly be due, at least in part, to the fact that such water readily acts as a carrier of salts. Of course field observations alone merely suggest lines of attack for problems such as this; they do not solve them. In this particular case, further knowledge of the chemistry of the soils in question, coupled with experiment, can alone decide the relative importance of aeration, acidity and the percentage of mineral salts.

(c) **Historical.** Across the centre of the moor, from its eastern border to Llwyn-y-garreg on the west, runs a discontinuous belt of *Pinus sylvestris* (Fig. 4). In some parts the trees are solitary and only occur at rare intervals. Towards the east they are more numerous, and are evidently multiplying quite naturally, for seedlings and young plants of all ages are plentiful³. The living pine trees do not extend beyond Llwyn-y-garreg (H, Fig. 4), but on the foreshore, between tide-marks, and forming as it were an extension of the pine-belt, is the "submerged forest" alluded to by Professor O. T. Jones. What is probably a continuation of the same buried forest is seen at low water in the bed of the artificial cut by which the River Leri now crosses the Dovey Flats (K, Fig. 4). Both on the foreshore and in the river bed, the majority of the tree-stools are still in the position of growth. This submerged forest has not yet been properly investigated, but many, perhaps the great majority, of the larger tree-stools on the foreshore undoubtedly belong to *Pinus sylvestris*⁴. The microscopical features of the secondary wood, and even the red colour of the bark so characteristic of this species, are well preserved. It may be a mere coincidence, but the relative positions of the living pines growing on the peat, and the buried pines beneath—the whole forming a nearly continuous belt crossing the bog from its eastern boundary to the foreshore—is suggestive. In view of the current opinion

¹ Tansley, *l.c.*, pp. 252 and 261.

² Jefferies, *l.c.*

³ Apparently the pines are extending over the moor in a westerly direction, though the prevalent winds are from the S.W. Prof. Jones makes the interesting suggestion that the seeds may be carried more easily by the dry easterly winds than by the moisture-laden S.W. winds. He points out that, for the same reason, the dust from lead-mine debris is mainly carried south-westwards, against the prevailing winds. In view of the fact that the seeds are liberated from pine cones only when dry, the suggestion seems plausible.

⁴ A submerged forest to the north, near Barmouth, appears to have consisted mainly of *Betula*. See Osborn, *Mem. Manchester Lit. and Phil. Soc.*, 56, 1912.

that in these islands *Pinus sylvestris* is native only in Scotland¹, it would be interesting to know whether or not the living pine trees found on the moor to-day are the lineal descendants of the ancient pines of the buried forest. The possibility of such a continuity cannot be ruled out on *a priori* grounds. It is conceivable that when wet moorland conditions came in, killing off the pines, their descendants retreated to the border of the Flats, extending on the surface of the peat whenever conditions became suitable. Of course on the other hand, it is equally, or perhaps more likely that the living pines have colonized the moor from some neighbouring plantation. The point is merely mentioned as one worth investigating.

Nothing is known about the earlier of the successive phases of the vegetation which appeared when the ice which once occupied the valley of the Dovey finally retreated. Professor Jones (see above) inclines to the view that the greater part of the valley floor became submerged, in which case much of the early vegetation may have been of the salt marsh type.

The first phase of which as yet we have any knowledge is that of the submerged pine-forest, which in all probability came into existence long after the glacial period. The former extent of this forest is at present quite unknown. It may have been extensive, or it may have been limited to the higher and drier areas of the Flats, the low-lying parts being occupied by other types of vegetation².

The forest was succeeded by a moorland phase, which may have commenced or extended owing to subsidence of the land. Moorland conditions still obtain over a considerable portion of the Dovey Flats, but the area of moorland has been circumscribed by the encroachment of the sea. Professor Jones has described above the gradual retreat of the coast-line, and the forming of the shingle beach. The latter has already passed the outlying portion of the ancient pine-forest, and wave action has almost completely destroyed its former covering of peat. A little, however, is still to be seen in places, overlying the tree remains. Not only has the sea destroyed the old western border of the peat-moor, but in many places along the Dovey and its tributaries, salt marsh, developed on a layer of estuarine silt, now overlies the peat³. How far this is due, on the one hand to subsidence, or on the other hand partly to a migration inland of the head of the estuary, still remains to be proved. At the present time, no doubt, this recession of the moorland is reduced to a minimum, owing to the artificial embanking of the Dovey and its tributaries, for the protection of the railway and for agricultural purposes.

¹ Cf. **Smith** in **Tansley**, *l.c.*, p. 116.

² The relative positions of the pine-belt and the probable pre-glacial course of the River Leri should be compared—Figs. 3 and 4.

³ Compare the moorland area in Fig. 4 with the distribution of peat shown in Fig. 3.

Systematic investigation would no doubt reveal much more of the history of the Dovey Flats than is outlined here.

This incomplete sketch of the vegetation of a highly interesting area would not have been published in its present form, had not my departure from the neighbourhood rendered it improbable that I could myself continue investigations which had been planned, but little more than begun. One of the reasons for its publication is the hope that it may prove of some slight assistance to future workers on this area.

For assistance of various kinds in connection with the preparation of this sketch, I wish to express my sincere thanks to my former colleagues, Professor O. T. Jones and Mr Stapledon. For some of the facts respecting the peat-moor I am indebted to Mr C. M. Green.

Mr Stapledon's earlier work having lain chiefly in the hill districts, the following account of the Dovey salt marshes represents the first serious effort to attack the ecological problems presented by the vegetation of the Flats of the Dovey valley. The work, which is of a preliminary character, was mainly carried out during 1914.

THE QUEEN'S UNIVERSITY,
BELFAST.

(To be concluded.)

NOTICES OF PUBLICATIONS ON FOREIGN VEGETATION

NEW ZEALAND VEGETATION

- (I) **Poppelwell, D. L.** "Notes on the plant covering of the Garvie Mountains, with a list of species." *Trans. New Zealand Inst.*, **47**, 1915, p. 120.
- (II) **Oliver, W. R. B.** "The vegetation of White Island, New Zealand." *Journ. Linn. Soc. Lond.*, **43**, 1915, pp. 41-47, 2 plates, 2 text-figures.
- (III) **Pegg, E. J.** "An ecological study of some New Zealand sand-dune plants." *Trans. New Zealand Inst.*, **46**, 1913, pp. 150-177, 7 figures.

(I) The Garvie Mountains, which rise in places to a height of over 6000 feet, are situated in Central Otago, New Zealand, and as they lie between the wet mountain region of the west coast and the drier eastern region their plant covering is of considerable interest. This is described by Mr Poppelwell, who ranges the plant formations under the headings forest, subalpine scrub, steppe, alpine meadow, rocks and cliffs, and bogs and swamps.

Forest. This is a beech forest, the dominant species being *Nothofagus menziesi* and *N. solandri*. Mixed with these is a larger number of other species of trees than is usual in beech forests. At the higher levels *N. fusca* is rather plentiful while a few trees of *N. cliffortioides* were noted. An interesting succession from *Leptospermum* heath to beech forest is recorded. Young *Nothofagus fusca* seedlings are plentiful in *Leptospermum scoparium* thickets, but where the beech outgrows its shelter the latter plant is destroyed by it.

Subalpine scrub. This in places is very dense and interwoven forming a close association of shrubs on the edge of the beech forest. The chief species include *Veronica buxifolia*, *Dacrydium bidwillii*, *Cassinia vauvilliersii*, *Dracophyllum longifolium*.

Steppe. Under this heading is included elevated parts covered with tussock meadow, the dominant grass being *Danthonia raoulii* with which is associated many herbaceous plants.

Alpine meadow. It is scarcely made clear how this differs from steppe, as it is described as a tussock meadow, the dominant species being *Danthonia flavescens* and *D. crassiuscula* associated with *Celmisia coriacea* and other herbaceous plants.

Bogs. A *Sphagnum* bog contains large patches of the rosette plant *Aciphylla pinnatifida*. This species, unlike the other members of the genus, sends out underground stolons from which the rosettes spring. It thus increases rapidly by a vegetative process and patches 1 to 2 m. in diameter all connected underground, though the surface rosettes are distinct, may frequently be found.

W. R. B. OLIVER.

(II) The vegetation described by the author is of interest because it grows under conditions hardly paralleled elsewhere in the New Zealand region, namely, in the presence of fumes of hydrochloric acid. White Island is a volcano which is in the solfatar stage and discharges immense quantities of steam; it is a small cone, 48 km. from the nearest point on the mainland, surrounded by water 330 m. deep, and since it is of comparatively recent origin it has probably never been united to the mainland and has thus received its plants by accidental dispersal. The water of the crater-lake contains on the average about 5 % hydrochloric acid. No vegetation occurs within or on the upper slopes of the outside of the crater. The vegetation occurs near the coast only, and usually in three definable belts. (1) The sea cliffs and coastal slopes support a low growth of grasses and

herbaceous plants; (2) next follows a belt of dense scrub, followed by (3) an open low shrub formation. The scrub belt which runs along the coast just above the cliffs varies in height from 3 to 8 m. and is composed of shrubs or small trees of *Metrosideros tomentosa*, of irregular habit but growing close together and bearing the dense dark green foliage at the top; no other species is seen except near the coast where patches of the broad-leaved tussocks of *Phormium tenax* may occur, with a few shrubs of *Coprosma baueri*. The author describes the structure of the leaves of the *Metrosideros* and the *Coprosma*, noting their distinctly xerophytic characters. Sea birds affect the vegetation to some extent; for instance the areas occupied by the gannet are quite clear of vegetation, the presence of dead plants of *Metrosideros tomentosa* in the midst of some of the colonies showing that the birds not only prevent the scrub from spreading but kill any on ground they may occupy. In parts of the spaces cleared by gannets there may however be a rank growth of herbaceous plants. Other areas are occupied by colonies of petrel which breed in burrows and undermine and overturn the soil. The vegetation on the cliffs and slopes not occupied by the birds is an open formation, with small patches of the fern *Histiopteris incisa*, the tussock grass *Poa anceps*, and the trailing succulent *Mesembryanthemum australe*; while a close meadow formation occurs in the areas annually occupied by birds, the rank herbaceous growth near the gannet colonies consisting chiefly of *Chenopodium triandrum* and *Sonchus oleraceus*.

(III) The authoress gives a historical summary of work previously published on the maritime vegetation of New Zealand, in particular the valuable investigations of L. Cockayne on the dune areas—indeed the present paper is intended to supplement Cockayne's account of the sand dune vegetation by giving details regarding certain individual species which have been studied anatomically. Although the authoress recognises clearly that anatomical and growth-form studies are insufficient apart from experimental work on transpiration and other physiological processes, the results presented are of great interest.

The beach area studied, near Canterbury, has along the greater part of its length a foredune or sand ridge, fixed to a large extent naturally but in part artificially by the native *Scirpus frondosus* and the introduced *Ammophila arenaria*. Inland from the foredune are unstable dunes, moist dune hollows and stable sand plains; the usual dominant on the active dune is the *Scirpus*, while farther inland the dunes become higher and the hollows deeper and after rainfall there are numerous lakes of which some dry up but others appear stagnant and have a rich vegetation. A list of the indigenous species is given, with notes on their habitats; many introduced plants are found, especially on the table plain, and the tree lupin (*Lupinus arboreus*) covers extensive patches on both dunes and plain. The edaphic conditions taken as important in governing the form and structure of the sand dune plants are the moderately fine quartz sand; the availability of moisture at all times except for the superficial 12 cm. or thereabouts on the sand hills, the greater wetness of the hollows as compared with the hills owing to the proximity of the water table so that water may lie in pools on the surface for long periods, especially in winter; the presence of a humus layer in many places, at some metres depth in the hills but forming an upper thin soil in some of the hollows; the lack of nutritive salts. The chief climatic factors are the prevalent winds (east from the sea, north-west hot and dry, south-west cold and often bringing rain), the effects being the blowing of sand so that plants are liable to be buried and to suffer mechanical injury from sand drift, chilling of the soil, enhancing of evaporation and of transpiration; strong insolation; heating of surface sand intensely at times, while the substratum where moist remains cool at a slight depth; the fairly severe frosts from June to August, -10°C . having been frequently recorded. Analyses published by Kearney have shown that the beach sand contains a very small quantity of salt, hence the dune plants cannot be regarded as halophytic.

Of the indigenous species (over 40), 17 were selected for anatomical investigation, and

the results are given in each case under the headings of habitat, general growth-form and leaf anatomy, besides being arranged in a series of comparative tables. The general conclusions are that while certain species are strongly xerophytic in leaf anatomy, the plants as a whole show various anatomical features which are mesophytic and apparently antagonistic to their well-being; that in considering adaptation to environment leaf anatomy alone is insufficient but must be taken in conjunction with the special growth form of the species; that a strongly xerophytic growth form may permit mesophytic leaf anatomy (*Calystegia soldanella*, etc.); that the plants of the moist hollows are mostly marked mesophytes, as is natural in their environment, though some (*Carex pumila*, etc.) have xerophytic growth forms; that on the whole the dune plants studied appear to have a good deal of anatomical structure quite out of harmony with the environment, such structure being probably in some cases at least to be considered as a family characteristic rather than an ecological adaptation. It is noted that the three active-dune shrubs in the area studied—species of *Coprosma*, *Pimelea* and *Cassinia*—show a gradual transition, so far as leaf anatomy goes, from mesophytic to xerophytic in the order given, yet they all grow under exactly similar conditions and all three are of distinctly xerophytic habit.

SOME RECENT DESCRIPTIONS OF PRAIRIE VEGETATION

- (I) **Vestal, A. G.** "Prairie vegetation of a mountain-front area in Colorado." *Bot. Gaz.*, **58**, 1914, pp. 377–400, 9 figures.
- (II) **Vestal, A. G.** "A black-soil prairie station in north-eastern Illinois." *Bull. Torrey Bot. Club*, **41**, 1914, pp. 351–363, 7 figures.
- (III) **Pool, R. J.** "A study of the vegetation of the sandhills of Nebraska." *Minnesota Bot. Studies*, **4**, 1914, pp. 189–312, 15 plates, 1 map, 16 figures.
- (IV) **Pool, R. J.** "Invasion of a prairie grove." *Proc. Amer. For.*, **10**, 1915, pp. 1–8.
- (V) **Weaver, J. E.** "A study of the root-systems of prairie plants in south-eastern Washington." *Plant World*, **18**, 1915, pp. 227–248, 273–292, 18 figures.

(I) This appears to us to be one of the most important publications in recent years dealing with the prairie vegetation of North America, since it contains not only the results of the author's studies, carried on in a Colorado district during three seasons, but also a general discussion of prairie vegetation with special reference to the classification of prairie plant communities.

The author's special study is that of the plant associations of the Great Plains region and of their modifications along the mountain-front due to climatic, physiographic and vegetational differences whose influence is exerted mainly in the area immediately adjoining the foot-hills and to a less degree within a mesa belt extending eastward for several miles from the mountains. The Great Plains are essentially a rocky slope covered by debris from the Rocky Mountains; erosion has in places removed the debris, exposing the underlying shales or sandstones with their residual soils, while the uneroded areas are left as raised benches, the mesas. The physiographic divisions of the area studied are (1) the foot-hills, with their hogback ridges and upturned crags, variable as to exposure, slope, soil character, etc.; (2) the mesas of the older and higher level, not continuous along the mountain-front; (3) the mesa terrace, a more extensive, lower and more recently graded surface; (4) the floodplain, of the present and still lower stream grade, usually

debris-covered like the two mesa levels; (5) the plains proper, usually separated from the mountain-front and with fine soil of residual or aeolian origin. In the open plains the plant associations are well defined, and various writers have contributed to the elucidation of their relations to soil and topography; but near the mountains they are more numerous, variable, mixed in character and not so definite. Among the conditions suggested by the author as tending to complicate the character of the vegetation are the following: the climate conditions undergo a transition at the junction of plains and mountain regions; annual climate fluctuations are here unusually great, favouring alternately mountains and plains vegetation; the rainfall during April and May is adequate for mesophytic prairie-grass vegetation, while the latter part of summer is usually dry, hence less xerophytic foothill plants are conspicuous in the mesa areas during the vernal period while later the xerophytes of plains and dry prairie-grass predominate; variability of soil conditions (texture, water content, run-off, etc.) is considerable and very local, making possible local and extreme variability in character of vegetation, plants of radically different growth-form and physiological constitution occurring frequently in association; topography is considerably and very locally diversified; there is abundant opportunity for invasion by mountain plants; environmental conditions are on the whole severe, hence the vegetation is largely open, and since open associations are less definite in plant composition than closed ones, in which competition has exerted greater selective influence, different associations are as likely to intergrade as to alternate sharply, especially as the environments often pass gradually one into another; present tendencies towards stabilisation of mesa vegetation are obscured by artificial factors, chiefly grazing. The main effect of these complicating agencies is that mixed associations are frequent, in which plants normally dominating different associations occur together, the various secondary species also not being so regularly associated with particular dominants as would be expected from the study of more nearly typical examples of these same associations in other parts of the prairie region. Only a tentative arrangement of the variations of associations is possible, the associations being characterised partly from their occurrence and composition in other parts of the prairie province. While certain communities in the mesa area are typical in composition, some are better regarded provisionally as mixtures of two associations or as representing one association varying in the direction of another or with an added plant element from some particular source; on the other hand certain appearances of some of the associations are of quite definite composition, occur regularly and uniformly in different stations of the mountain-front, and can be definitely correlated with particular environmental features.

The author takes the unit of vegetation to be the association, an essentially uniform assemblage of plants living together in an area essentially uniform in environmental conditions, uniformity not being taken to exclude internal *local* variability of environment or vegetation; and he points out that certain attributes of associations formulated by those who have worked principally with closed vegetation in the humid eastern states will not apply to open growth in the less favourable environments of semi-arid regions, or to primitive stages in development of vegetation, or to mixed growths in habitats internally variable. In areas of permanently or temporarily open vegetation, plant competition is usually not an important limiting factor, there being no competition for light as in forest and very little for above-ground space as in closed grassland, while root competition is probably not so general as accommodation of root systems so that different species derive moisture from different depths; hence physical conditions may exert more direct control upon plant individuals. The author considers it advisable at present to make our concept of the plant association quite broad, and to recognise that there are different types of associations. In his classification of prairie associations (see below) he

makes use of no single criterion; as he points out, the associations within a particular region form a complex which may be classified in different ways according to the purpose of the study. He uses the term *consocieties* to denote an appearance or representation of an association characterised by one or several of its *dominant* species; British writers use *facies* in the sense that the author uses *consocieties*, and Gleason who introduced the latter term has given criteria for determining whether two communities represent distinct associations or two *consocieties* of the same association. A *society* of an association is taken by the author to mean a representation of an association distinguished by abundance of one or several *secondary* species. "Some ecologists would use *society* in the sense that *consocieties* is here used, preferring to use *consocieties* as synonymous with association, reserving the latter term for referring generically to plant growths in general." But surely "community" is as good a general colourless non-committal term as "growth" which the author uses. The author thus distinguishes between communities characterised by dominant species and secondary species respectively by calling the first a *consociety* and the second a *society*; as he remarks, there may be a number of different kinds of societies.

The author then describes the associations occurring typically within, and usually restricted to, the generally treeless interior region of North America which is characterised by low winter rainfall and is termed the prairie region or province; practically all the associations show considerable variation over their range, which is in most cases extensive. His arrangement (here modified so as to begin with the primitive types) is as follows:

I. Minor Prairie Associations.—Associations of local, though commonly wide, distribution within the area of the province; either established or primitive stages of vegetation; frequently not restricted to the area of the province.

A. Primitive Associations.—Associations not typical of particular habitats, but scatteringly distributed chiefly because they are *primitive growths*; early stages in development of vegetation; growths typical of recently denuded or broken surfaces, or of physiographically new environments. Vegetation temporary in character; usually tending to change more rapidly than physical environments.

1. Growth dominated by annuals; short-lived growths typical in recently disturbed areas. *Plains Ruderal Association*.

2. Growths dominated by perennials; frequently preceded by a ruderal stage; usually less temporary in character.

(a) Dominant plants xerophytic bunch-grasses. *Primitive Bunch-grass Association*.

(b) Dominant plants bushy xerophytes, deep-rooted, not grasses. *Gutierrezia-Artemisia Association*.

B. Local or Edaphic Associations.—Associations typical of habitats representing extreme conditions within the area of the province, in which *local* physical conditions, not being in accord with climatic conditions, determine the character of the vegetation to a large extent. The growth is thus as stable and permanent as the physical environment.

1. Associations of rock or of non-alkaline soils.

Growth of rock surfaces; well developed only in the foothills. *Lichen Association*.

2. Associations of dry soil.

(a) In stony or gravelly habitats, as buttes, rock ridges, and exposed mesa-crests.

(i) In the most extremely xerophytic and stony habitats; dominant plants cespitose, prostrate. *Mat Association*.

(ii) In less extreme habitats of coarse or loose soil; dominant plants xerophytic grasses. *Stipa-Aristida Association*.

(b) In sandy soil; not well represented within the area studied. *Sand-Hills Mixed Association*.

3. Associations of soil of high water content.

(a) In moist soils, usually bordering depressions. *Hordeum jubatum* Association.

(b) In wet or submerged soils. *Swamp Associations*, etc.

4. Associations of saline or alkaline soils.

In deep dry alkaline soil, frequently sandy; growth dominated by tall xerophytic shrubs. *Chrysothamnus-Sarcobatus* Association.

II. Climatic or Major Prairie Associations.—Associations of extended and general distribution within the area of the province; established vegetation, relatively stable or permanent, occupying the more extensive habitats provided by climate and physiography.

A. Growth dominated by surface-rooted grasses, extensive in the more arid western part of the province, or Great Plains region.

1. Dominant plants of low mat form. *Short-Grass Association*.

2. Dominant plants taller; growth extensive in northern parts of the plains region and extending southward locally along the mountain front. *Wheat-Grass Association*.

B. Growth dominated by usually deep-rooted grasses; more extensively developed in the less arid central and eastern parts of the province, and of local distribution along the mountain-front.

1. Dominant plants of tuft growth-form (of the *Andropogon* type); many of the secondary species pronounced xerophytes; growth most extensively developed in the central part of the prairie region. *Bunch-Grass Association*.

2. Dominant plants close-growing mesophytic grasses, usually sod-formers (of the nature of *Poa pratensis*); secondary species composed of a larger proportion of mesophytes; most extensively developed in the eastern part of the prairie region, particularly along the forest border. *Prairie-Grass Association*.

In the plains ruderal association the first plants to invade disturbed ground in the area studied are annuals, practically all of the plains region and comprising species of *Argemone*, *Euphorbia*, *Solanum*, *Festuca*, *Plantago*, *Helianthus*, etc. In the primitive bunch-grass association, certain grasses of the prairie region are abundant in new growths or in open or sterile situations, as contrasted with other grasses found only in more permanent, closed associations, or in mesophytic stations or in soils of considerable humus content; among these xerophytic grasses distinctive in primitive growths are species of *Calamovilfa*, *Sporobolus*, *Elymus*, *Panicum*, etc., all capable of growing in coarse soil, being deep-rooted, and some of them building temporary dunes on the sand-hills and on the shores of the Great Lakes. The *Gutierrezia-Artemisia* association is typically developed in the plains areas of the region studied, *G. sarothrae* being more abundant in the southern part of the plains region while *A. frigida* ranges far north and forms an important primitive growth in the mountains as high as 10,000 ft., hence the *A. frigida* consociates is the important growth of the mountain-front, being frequent on talus slopes and gravel slides of the foot-hills.

The lichen association on rock surfaces contributes an element to the vegetation of detrital soils of the higher mesa and mesa-terrace levels in the region studied; surface rocks are present on nearly all the mesa-tops; the dominant species are *Parmelia conspersa*, *Rinodina oreina*, *Lecanora calcarea* and *L. subfusca* var. *allophana*. The mat association or open growth of dwarfed perennials which occupies sterile gravelly situations is physiologically similar to the *Gutierrezia-Artemisia* association, but is distinctive in growth-form and in not occurring in such extreme conditions of coarse soil and sun and wind exposure; the distinctive plants are species of *Townsendia*, *Orophaca*, *Lesquerella*, *Paronychia*, *Gilia*, etc. The dominant plants of the *Stipa-Aristida* association are xerophytic grasses of tuft growth-form with moderately deep roots, growing usually in coarse sterile soil; the *Stipa comata* consociates occurs on gravelly slopes and on wind-swept tops and crests of mesas;

the *Aristida longiseta* consociates is important in sandy loam and broken soils in eastern Colorado, Kansas and Nebraska, but in the mesa region the species does not occur except in association with other grasses, chiefly *S. cometa*. The sand-hills mixed association is not typically developed in the area studied, there being no truly sandy areas of any extent, but sandy soil may be recognised by the presence, often in abundance, of *Mentzelia nuda*, *Abronia fragrans*, *Cleome serratula* and *Artemisia filifolia*. The *Hordeum jubatum* association typically forms a pure growth occupying moist soil of depressions, or a zone of soil around swampy areas or standing water, or bordering gently sloping ditch-banks. The *Chrysothamnus-Sarcobatus* association occurs in deep alkaline soil, usually loose or sandy; *C. graveolens* is more abundant in loam, *S. vermiculatus* in sandy loam or sand, and the two often dominate together. The salt-grass association, with the two grasses *Sporobolus asperifolius* and *Distichlis spicata* dominant singly or together, is developed on flats which are sometimes white with alkali and occur on sloping margins of floodplain lakes and irrigation reservoirs and in restricted stream bottom areas; irrigation tends to increase their number and extent; the soil is clay or loam; *Suaeda diffusa* may occur in similar habitats though usually the clay is dry and loose, and may represent either a distinct association of strongly alkaline or saline habitats or a primitive growth of alkaline soil. The author notes that though primitive and local associations cannot always be sharply separated it seems best to distinguish the two groups. For instance the *Gutierrezia-Artemisia* association, while most frequent in gravelly mesa-tops, is a primitive growth rather than an association of this particular habitat; in such situations it normally develops into the short-grass association. On the other hand, certain appearances of the *Stipa-Aristida* association may be, following conditions of disturbance, a primitive association. Local associations, or communities relatively permanent in extreme habitats, may become primitive or temporary associations in the less extreme habitats in which climatic conditions are dominant except for a short time after disturbance.

The short-grass association is typically developed on the open plains, but near the mountains and in the northern part of the plains region the buffalo-grass, *Buchloe (Bulbilis) dactyloides*, is very scanty as compared with the grama-grass, *Bouteloua oligostachya*; the latter may either form a pure or nearly pure growth (*Bouteloua* consociates) or in the coarse soil of the mesa-terrace may enter into a mixed growth characterised by abundance of the deeper-rooted perennials of the plains region (*Euphorbia robusta*, *Psoralea tenuiflora*, etc.) together with (1) deeper-rooted grasses, (2) tall composites, legumes, etc., typical of the more xerophytic prairie-grass east of the plains region, (3) less xerophytic plants from the foot-hills. This *Bouteloua* mixed consociates, representing the most radical departure from the typical short-grass, really differs mainly in the possession of a derived element, for local patches of pure short-grass are still present and the mesophytic plants are found in local spots differing in moisture conditions due to the extreme mixture of all sizes of soil constituents. The wheat-grass association, dominated by *Agropyron Smithii* (*A. occidentale*), is established in looser clay soil than that in which the short-grasses dominate, the typical habitat being the deposition area at the base of side-slopes of mesas with fine soil washed down from above; invasion by grama-grass is often initiated and an intermediate *Agropyron-Bouteloua* community formed; definite societies are formed by *Astragalus goniatius* and *Artemisia gnaphalodes*, by *Astragalus drummondii*, by *Artemisia aromatica*, and by *Carex stenophylla* and *C. pennsylvanica*. The bunch-grass association though occupying a small part of the area studied is similar in composition to that extending over the prairie province, the species dominating together in the order of importance *Andropogon scoparius*, *Koeleria cristata*, *Andropogon furcatus*, *Sorghastrum nutans*, *Muehlenbergia gracilis*, *Antheropogon curtispendus*, while secondary species include other grasses and rather xerophytic prairie perennials such as species of *Liatris*, *Gaillardia*,

Psoralea, *Aster* and *Chrysopsis*. This association depends on a constant water supply enduring through the latter part of summer, and as available soil moisture is constantly present in mesa-terrace soils only till about mid-July it is limited to moist slopes, the higher mesa-tops and small depressions; it includes a consocieties composed of pure or almost pure *Andropogon furcatus*, a similar *A. scoparius* consocieties, and one with *A. furcatus* and *Sorghastrum nutans*. The prairie-grass association is in the area studied a mesophytic and meadow in spring, becoming quite dry in late summer when most of the plants have died down, and it is typically developed in rich black soil of fine texture and high water content in spring and early summer, such soil being found in alluvial lower slopes of foot-hills and higher mesas. The author points out that the prairie-grass locally found west of the plains belt has many features in common with eastern black-soil prairie (see II, below) as represented along the border of the eastern deciduous forest, but the secondary species are mostly different, and the growth found along the mountain-front might be considered a separate (western mesophytic prairie-grass) association which perhaps intergrades with the prairie-grass of the middle part of the prairie region. A growth on what is called the middle mesa is intermediate between short-grass and prairie-grass, and is floristically similar to the prairie-grass described for South Dakota by Harvey.

(II) The author here describes an example of a very luxuriant prairie type, the mesophytic prairie-grass of the eastern border of the prairie region, a type especially well developed in the upper Wisconsin glaciation area of north-eastern Illinois. Small scattered areas of this type of prairie were formerly abundant west of Chicago, but in recent years they have suffered greatly from human interference. In its original condition established black-soil prairie of this eastern type may be regarded as luxuriant grassland with a rich flora and many local facies due to local dominance or abundance of one or several species. The surface is usually undulating, streams are few so that depressions have very wet or submerged soil while elevations may be very dry and the local variation in soil moisture is thus considerable. The species composition changes with soil moisture and a complete transitional series of prairie growths can be recognised. The mean and the two extremes of the series may be regarded as forming three distinct associations—xerophytic and mesophytic prairie-grass and hydrophytic or swamp prairie or fen—but these intergrade instead of alternating sharply, many species tolerating a wide range of soil moisture and of other environmental conditions so that some occur abundantly in more than one association while others reach greatest abundance in transitional growths intermediate between two associations. The xerophytic prairie-grass association is best represented in the region studied by the *Silphium laciniatum* consocieties where it displaces *Andropogon scoparius* from dominance. The mesophytic prairie-grass association, more widely distributed in the area, has several well-defined representatives, one dominated by *Andropogon furcatus* with often hardly any other species present, a second dominated by a number of grass species (mixed consocieties), and a third by the large rosin-plant *Silphium terebinthinaceum* and grasses. The hydrophytic extreme of prairie-grass passes insensibly in places into marsh associations, though in other places there is conspicuous zonation, the boundaries following contour lines around depressions; a distinctive appearance of this swamp prairie is the *Liatris spicata* consocieties, there is also a mixed consocieties of variable composition in which umbellifers are frequently prominent, and the meadow-rue *Thalictrum dasycarpum* sometimes marks a well-defined zone. The *Eryngium* consocieties of swamp prairie, corresponding fairly well with the low prairie of Cowles, shades into the *Silphium terebinthinaceum* consocieties of mesophytic prairie-grass, the two plants being frequently seen together in about equal abundance, so that this is the transitional growth between hydrophytic and mesophytic prairie. The author gives lists, with frequency annotation, for all these types. In dealing with the development of prairie he points out that mesophytic black-soil

prairie may arise from either of two extreme types of vegetation, hydrophytic or xerophytic. Successions from marsh to prairie have been described by Cowles and by Gates, and the development of xerophytic prairie into less xerophytic types by Gates and by the author. The development of mesophytic prairie from both xerophytic and hydrophytic extremes may be due to action of the vegetation itself or to physical changes in environment; retrogressive successions occur locally; and relic species from the former condition are perhaps more abundant than invading species, so that apparently change in floristic condition lags behind changes in ecological conditions, owing to greater or less plasticity of environmental reactions in most of the plant species.

(III) The sandhill region of Nebraska extends over the great area of about 18,000 sq. miles, nearly one-fourth that of the whole state; similar regions occur in the neighbouring states of Kansas, Colorado and South Dakota but are much less extensive and do not form such a striking feature of the landscape. The soil is dune sand, evidently derived from Tertiary deposits, and many of the ancient dunes after undergoing stabilisation and occupation by vegetation have through human interference—chiefly by fires and excessive grazing—reverted to their juvenile and mobile condition. The author's account is marked by the care and thoroughness characteristic of most American ecological investigations. The description of the vegetation is preceded by data, obviously the outcome of a vast amount of detailed measurement work, regarding precipitation, wind, evaporation, temperature and other ecological factors, and we cannot sufficiently commend also his freedom from the dogmatism and cocksureness concerning the classification and designation of plant communities which marks, and mars, too many regional surveys nowadays. He justly criticises the too free and vague use of the term "formation," rightly pointing out that this term should be used with caution and applied only to the larger and more sharply contrasting vegetation units, and that too often it is used where the term association would be more suitable. The prairie-grass formation of the uplands stands out in sharp contrast with the short-grass formation of the plains, the two together comprising the majority of the main climatic grasslands lying between the eastern forests and the mountains. The two agree generally in physiognomy but have different component species, and the author makes out a good case for concluding that the limiting or differentiating factors are the available water on one hand and competition on the other—not temperature as Merriam suggested. The chief component of the prairie-grass formation is the bunch-grass (*Andropogon scoparius*) association, representing the temporary climax vegetation of the region and that which prevailed before its settlement by white men. It is an open community, the grasses growing in tufts, but probably some closed prairie-grass community will eventually prevail and supersede it—evidence for this view was obtained from examination of the spear-grass association (dominants *Stipa comata* and *Koeleria cristata*) and in the grama buffalo-grass association (dominants *Bouteloua* and *Bulbilis*). The chief interest in the author's dynamic vegetation study, however, lies in the retrogressive phases as represented by the blow-outs, arising mainly from fires and grazing. When the plants die out patches of bare sand are left, usually small at first. Then the sand in these patches is scooped out by wind, forming conical crater-like hollows—the blow-outs. As the scooping-out process continues, sand falls in from the sides, so that the blow-out increases both in area and depth until it may reach a depth of 100 ft. and a circumference of 600 ft. Finally, wind erosion is checked, a foothold is gained by pioneer species like *Calamovilfa longifolia*, *Psoralea lanceolata* and *Redfieldia flexuosa*; these pioneers are followed by the bunch-grass association, after which vegetational changes are much less rapid. An interesting feature in the woodland formations along streams is the overlapping of the deciduous eastern forest and the western yellow pine (*P. ponderosa*) forest. The lowland formations resemble those found elsewhere both as to composition

and succession, save that a meadow type represents the temporary climax, one of the more eastern of the prairie-grass associations probably representing a more ultimate climax.

(IV) In this interesting preliminary report the author describes the conditions existing in a portion of high prairie near Lincoln, Nebraska, where forty years ago a grove was started by furrows being run at intervals of 4 to 6 feet through the prairie and tree seeds dropped into the furrows. The grove, which consists of about 20 acres forested with *Fraxinus pennsylvanica*, *Juglans nigra*, *Ulmus fulva*, *Acer saccharinum* and *A. negundo*, has never undergone cultivation nor damage by fire or grazing, hence it offers on one hand a demonstration of the fact that trees grow freely once they are planted in prairie soil, although naturally they rarely invade these grasslands, and on the other a good opportunity of studying the changes in the ground vegetation resulting from the altered conditions due to tree growth. The original prairie sod has disappeared with nearly every original prairie species, and of the invading species (about 90) which have replaced the original vegetation 85 % are mesophytic in character and 60 % distinctively woodland forms. In this rapid transformation of prairie into forest many factors have evidently been involved—changes in soil moisture, evaporation rate, light intensity, etc.—and these are now under investigation.

(V) While engaged in a study of the plant communities of semi-arid south-eastern Washington the author felt that a knowledge of the root-systems of the more important prairie species was necessary for a proper understanding of the development and structure of these associations and in this paper he gives the results of his examination of the roots of twenty-five of the chief species, with a discussion of the conditions under which the plants grow.

The prairies of south-eastern Washington and their eastward extension into adjacent Idaho occupy a position between the foot-hills on the east and the sage-brush region on the west; on the south they are bounded by the high lava-rock upfold of the Blue Mountains, while northwards the Spokane gravels with their open growth of yellow pine mark the general northern boundary of the great lava sheet and its accompanying prairie formation. As the Columbian Plateau with its wind-moulded hills ascends to 2700 feet near its eastern border, the precipitation increases and this is reflected in a more highly developed type of prairie vegetation; in fact the well-developed huge prairies occupy a relatively narrow belt of 30 to 50 miles width along the eastern edge of the plateau, while the area westward is characterised by a very open type of bunch-grass vegetation. Hemmed in on all sides by mountains and especially cut off from the moist winds of the Pacific by the Cascades, the Columbian Plateau has a very low annual precipitation, in much of the area less than 10 inches, and even where the prevailing south-west wind, cutting through the mountain gap of the Columbia River and rising over the great High Plains, loses much of its moisture near the high eastern border, the annual precipitation is only 21 inches. In such a semi-arid region where evaporation rates are very high, the distribution of rainfall and humidity is important since scanty rainfall throughout the year or relative dryness of the air and soil during the growing season favours a sparse vegetation and the development of xerophytic forms. Over two-thirds of the precipitation occurs during the non-growing season, and the light showers of July and August seldom have much influence on the soil water content. The soils of this region, a good representative of high prairies in general, may be compared to a gigantic reservoir replenished mostly during the non-growing season and rather thoroughly emptied of its water during summer. It is not the absolute rainfall figures alone that furnish a criterion of climate since the maximum duration of the drought period forms a limiting factor of the greatest importance. The great problem is the extent to which soil water derived from winter precipitation is conserved through the weeks of drought. The rains in south-eastern Washington are so gentle that there is practically

no run-off, and the silt-loam soils are very retentive of moisture. As pointed out by Shreve see this JOURNAL, 3, 1915, pp. 43-44), the influence of rainfall upon the distributional and seasonal activities of plants is obviously exerted chiefly through its power to replenish soil moisture, and while rainfall is only mediate in its relations to plants soil moisture is immediate.

The author gives data and graphs to illustrate the seasonal march of soil water, one of the most striking points brought out in these being the contrast between the exposed south and south-west slopes and the steeper north and north-east leeward slopes. The latter have more clay and more humus, this combination being reflected in the increased water-holding capacity of the soil; an average of several determinations gave a mean water-holding capacity of 56 % (based on dry weight at 104° C.) for the first foot of soil on north slopes as compared with 48 % on south slopes, and this margin is a rather important difference in favour of the soils on the protected slopes since the wilting coefficients of the two soils differ but little. Apart from the greater amount of moisture on the north-east slope, in some cases twice that of the south-west slope, the soil on the exposed slope reached its wilting coefficient by the middle of July about five weeks before the sheltered slope. The data show that prairie plants must obtain their water from greater depths than 10 inches, at least during the dry summers; some of these plants penetrate to 12 feet, while most of them get the bulk of their water from the second to the sixth foot of soil, hence a consideration of soil moisture at these depths becomes important. Determinations made from early spring till late summer showed that there was still a downward movement of water at depths of 4 and 5 feet after the middle of April, but from early June to mid-August the soil moisture was gradually depleted at all depths to 5 feet. The observations emphasise the fact that "topography with soil texture is the great middleman that distributes the soil moisture to fill the gigantic earthen reservoir, which again is largely emptied during the following growing season." Temperature records showed that on both slopes the seasonal march of soil and air temperatures varies inversely with the soil water, that is, the temperatures steadily become higher in proportion as the soils become drier. A comparison of soil temperature readings at 1 foot depth on the two slopes showed that at this depth the daily range is rarely over 1° F., that the south-west soils are from 3° to 5° F. warmer in early spring than those of the north slopes, and that these differences may increase by late summer to 7° to 10° F.; the higher soil temperatures prevailing on the south side have obviously much to do with the earlier seasonal activities of many plants, for several were found to flower 10 to 17 days earlier on south than on north slopes.

From a continuous record of humidity taken during more than two complete growing seasons it was found that the air is often 5-10 % drier on the exposed than on the sheltered slopes, and that sometimes on the dry slopes and during late afternoons the humidity might fall to 15-30 % and rise again during the night to 75 or even 95 %. The wind, prevailing from the south-west, is important to vegetation because it increases the evaporating power of the air, and the greater saturation deficit increases transpiration. Anemometer records showed that a total of over 13,000 miles of wind passed over the south-west slope at a height of 0.5 m. while only about half as many miles were recorded at a similar position on a north-east slope. These factors of temperature, humidity and wind may be satisfactorily summed up, however, by measuring the evaporating power of the air, and atmometer records showed that from early May to late September the average daily evaporation on the north-east prairie slopes was only 64 % of that on south-west exposures.

In order to determine the depth at which the chief prairie plants obtain their water supply and to get accurate data on the distribution and extent of the root systems in the soil, the author undertook extensive trenching operations, sometimes to a depth of 10 or

12 feet, so as to obtain vertical faces from which the root system could be excavated in its entirety. In the course of the work the importance of the work of earthworms was evidenced by the fact that the soils were often literally honeycombed with holes ranging from 7 to 8 mm. in diameter and reaching depths of over 13 feet; obviously these burrows play a large part in the penetration of soil water and doubtless also in affording additional aeration in fine-textured soils like those examined. Details are given of the root systems of 25 species, more than 350 systems in all being examined. In his discussion the author points out that the most striking and obvious result of his observations is the fact that the plant's response to the severe environmental conditions in the area investigated is a well-developed and extensive root system; for just as the evaporating power of the air and the nature of the transpiring organs determine the water requirements of plants, so the soil water and the nature of root systems determine the water supply. It is noted however that while the condition of light summer rainfall is unfavourable for shallow-rooted grasses, still three of the most important prairie grasses are shallow-rooted. Of these *Poa sandbergii*, the first to appear on thin soils where the underlying rock is little broken, is on the prairie an important interstitial plant, but the shallow-rooted *Koeleria cristata* and *Festuca ovina* play an important part in the deep soils of the prairies. The water-holding capacity of the soils favours these shallow-rooted species, but the deep-rooted *Agropyron spicatum* early assumes importance as a crevice plant where sufficient cleavage of the rock has occurred, this species becoming dominant in the bunch-grass association where thin soils overlie decomposed basalt, while on the prairie it partly abandons the bunch habit and may become more or less of a sod-former. It is noted that according to Cannon's classification all the root systems here described fall under the generalised type, that in which both tap and laterals are well developed, so that the roots penetrate deeply and reach out widely. The author's observation of great root depths correlated with deep soil moisture bears out Cannon's suggestion of the probability that the longest or most deeply penetrating roots are found not in deserts but where there is considerable rainfall and where the penetration of rain is considerable and the water table relatively deep. Shantz in his studies on the Great Plains found that the prairie-grass formation, characterised by the deep-rooted *Andropogon scoparius*, *A. halli*, *Psoralea tenuiflora*, *Redfieldia flexuosa*, etc., is limited in its western extension by insufficient deep water supply and is replaced by the shallow-rooted short-grass formation.

As the author remarks, the neglect of most ecologists in not working in this interesting field is to be deplored, though we must not overlook the fact that the real solution of the problem of adaptation to environment will be obtained only when the extent and character of both the absorbing and the transpiring organs of plants are studied and correlated.

VEGETATION OF THE TOOELE VALLEY, UTAH

Kearney, T. H., Briggs, L. J., Shantz, H. L., McLane, J. W., and Piemelsel, R. L. "Indicator significance of vegetation in Tooele Valley, Utah." *Journ. Agric. Research*, **1**, 1914, pp. 365-417, 7 plates, 13 text-figures.

This is an excellent example of a thoroughly well planned and executed piece of ecological research, in which detailed quantitative determinations were made for the various measurable environmental factors, such as perhaps would hardly have been possible for a smaller number of co-workers to have carried out within a moderate period of time.

The authors point out that while the study of native vegetation from the "indicator" point of view—the determination and correlation of the distribution of the vegetation with the physical and chemical properties of the soil, such as may be utilised in the classification of land with reference to its agricultural possibilities—has been long extensively carried on in Europe, especially as regards the so-called lime-loving and lime-avoiding plants, until recently comparatively little had been done in this direction in the United States. To this we must add, however, that such work has certainly never been done so thoroughly as in the United States; for instance, Shantz, one of the authors of this paper, in 1911 described the correlation existing in the Great Plains between the different vegetation types and the physical characters of the corresponding soil types, and pointed out how the native growth may be used in that region to determine the suitability of the land for dry farming.

The present paper deals with investigations in the Great Basin area, the portion of the United States lying between the Rocky Mountains on the east and the Sierra Nevada and Cascade Range on the west. The object was to determine (1) what types of vegetation indicate soil conditions favourable or unfavourable to dry farming, (2) what types indicate presence or absence of alkali salts in quantities likely to injure cultivated crops. A locality was necessary in which both dry farming and irrigation farming are practised, where much of the land is still covered with the original vegetation, and where some at least of the soils contain an excess of alkali salts. The Tooele Valley in central Utah was chosen because several very distinctive vegetation types are found within a small area, the soils show great diversity in moisture conditions and salt content, and the greater part of the area retains its original plant covering while examples of crop production both with and without irrigation exist on different types of land.

Soil samples were taken, to a depth of 4 feet or more, in the area occupied by each vegetation type, and the measurements of moisture content, moisture equivalent, electrical resistance and salt content made on these samples served as a basis for conclusions regarding the edaphic conditions indicated by the presence of each chief vegetation type. Each sample was weighed fresh and then dried to constant weight; the moisture content is in all cases expressed as a percentage of the dry weight of the sample. The method of moisture equivalents, previously worked out by two of the authors as a means of obtaining a standard for measurement of the retentivity of the soil for moisture, consists in subjecting the moist soil to a constant centrifugal force equal to 1000 times that of gravity until the moisture content is reduced to the point where it is in equilibrium with the force used; this value, expressed as a percentage of the dry weight, is the moisture equivalent. This value serves as an indirect means of determining the wilting equivalent, which denotes (as a percentage of dry weight of soil) the quantity of water remaining in the volume of soil occupied by the active roots of a plant which is beginning to wilt. The total salt content was determined by an electrical resistance method.

The climate of the Tooele Valley is dry, the mean annual precipitation being only 16 inches. The precipitation occurring during the months from October to May probably furnishes all the soil moisture available for the growth of plants during the following summer, for while the summer months are not rainless the great increase in the rate of evaporation in summer (that for June to August is at least double that of April and October) is such that the light precipitation can have but little effect on vegetation. In those parts of the valley where the ground water is beyond the reach of plant roots the vegetation becomes dormant after the moisture stored in the soil by the winter and spring rains has been exhausted. Herbaceous plants ripen and die, at least to the ground, while woody species after losing much of their foliage and reducing transpiration to a minimum enter a resting condition which is nearly as complete as that brought about by the low

temperatures of winter. The soils show a wide range in salinity (alkali content), those in the upper broad end of the valley having a low salt content while those of the flats near Great Salt Lake itself sometimes contain such an excess of salts as to prevent the development of any plant covering. In the central part of the valley the soils are relatively free from salts in the surface foot, but the salinity of the subsoil is so great as to exclude all deep-rooting plants save those which are salt-tolerant in a marked degree. Sodium and chlorine together constitute about 90 % of the total soluble material in the Lake, the rest being almost entirely made up of potassium, magnesium and the sulphate radicle. Calcium and to a less extent sodium carbonates were found widely distributed in the soils of the valley, though absent from the Lake water. As might be expected, the chlorides were the commonest and most widely distributed of the soluble constituents of the soils.

The vegetation of the area is typical of a large part of the Great Basin and is characterised by the great extent of the areas occupied continuously by a single type of vegetation, the sharpness of the boundaries between the areas occupied by the various types, and the great predominance of one or very few species in each type. The authors distinguish five associations—sage brush (*Artemisia dentata*), sand-hill mixed (*A. tridentata*, *Juniperus utahensis*, *Chrysothamnus nauseosus*), Kochia (*K. vestita*), shadscale (*Atriplex confertifolia*) and greasewood-shadscale (*A. confertifolia* and *Sarcobatus vermiculatus*)—and two series of communities, using this non-committal term pending the further investigation required before definite ecological rank can be assigned to the grass-flat (*Distichlis*, *Sporobolus airoides*, *Chrysothamnus graveolens*) and the salt-flat (*Allenrolfea occidentalis*, *Salicornia utahensis* and *S. rubra*) vegetation. Each of these is described in detail, with data relating to topographical features, botanical composition, moisture conditions, salt content, adaptations to the physical conditions, etc. The sage-brush association covers the land nearest the mountains where the soil is of rather light texture, permeable, rather low in water-holding capacity and free from an excess of alkali salts, and where under natural conditions the moisture available for growth is usually exhausted early in summer. The Kochia association covers areas lying just below the sage-brush belt and also occupies islands in the midst of this vegetation; the soil is very homogeneous and of finer texture, relatively impermeable, of higher moisture capacity and with higher salt content in the subsoil; the first foot of soil is generally free from an injurious quantity of alkali salts, and available moisture is usually lacking during summer for a depth of at least 4 feet. The shadscale association occupies the land next below the Kochia belt, and though the soil is on the whole similar it often contains much gravel, is generally even drier in summer, and has somewhat smaller salt content. The greasewood-shadscale association forms a belt lying between the pure shadscale vegetation and the salt-flats, and also crowns the ridges and knolls that intersect the latter; the soil differs from that of any of the foregoing associations in generally containing during summer moisture available for growth at all depths below the surface foot, and it is also strongly saline below this depth. The presence of the grass-flat vegetation indicates a soil with a high moisture capacity, more or less saline, and moisture to the surface during the greater part of the year. The salt-flat vegetation occupies land which is extremely saline and is wet to the surface for a great part of the year.

ON THE ECOLOGY OF THE VEGETATION OF BRECKLAND

II. FACTORS RELATING TO THE RELATIVE DISTRIBUTIONS OF *CALLUNA*-HEATH AND GRASS-HEATH IN BRECKLAND

By E. PICKWORTH FARROW

(With Plates VI—VIII and one Figure in the Text)

It has already been stated that *Calluna*-heath alternates with grass-heath in Breckland and detailed descriptions of these two characteristic associations and a map of their distributions on Cavenham Heath have been given¹. One of the first problems which arose during the course of this Breckland work was to determine the causes of the relative distributions of these two main associations. This alternation of grass-heath with *Calluna*-heath in Breckland has previously been supposed to be due to varying proportions of lime in the soil². Examination of the upper strata of the soils of the grass-heath associations showed that they usually possess the dark chocolate coloured stratum at 20 to 35 cm. from the surface which is very characteristic of the *Calluna* associations.

During the examinations of the upper strata of the soils of the grass-heath associations on Cavenham Heath, some rather decayed remains of *Calluna* roots were found even near the outer edge of the grass-heath association, near the area marked 14 on the map of Cavenham Heath³, about half a mile from the main *Calluna* association. This was a surprising discovery, for it meant that *Calluna*-heath must once have existed on this spot which is now grass-heath, and that probably the *Calluna* existed in this position fairly recently, since organic bodies apparently decay quickly in this open sandy soil. A closer examination was therefore made of the transition zone where the grass-heath association changes into *Calluna*-heath. In this zone, as the typical *Calluna* association is approached from the grass-heath association, isolated plants of *Calluna* of small height begin

¹ Farrow, E. P., "On the Ecology of the Vegetation of Breckland," this JOURNAL, 3, 1915, pp. 211-228.

² "Types of British Vegetation," 1911, p. 107.

³ This JOURNAL, 3, 1915, p. 217.

to appear, and these gradually become more numerous and of greater height as the typical *Calluna* association is entered. This transition zone is also characterised by the presence of abundant *Cladonia coccifera*, *C. cervicornis* and *C. alcicornis* growing amongst the branches of the more dwarf *Calluna* plants (Plate VII, Photos. 3 and 4).

These phenomena were very puzzling for some time—the luxuriant *Cladonia* appeared to be smothering the *Calluna*. The clue to the matter was however given by an examination of the areas immediately around rabbit burrows which occur amongst the *Calluna* plants on the heath, as well as in the places occupied by various other associations. Immediately near the rabbit burrows the ground is often bare or is occupied only by dwarfed grasses. Just around these areas the *Calluna* bushes are much less in height than typical ones and have a smooth rounded appearance with no projecting shoots, and they become taller further away from the rabbit burrows. The small *Calluna* bushes in this zone around rabbit burrows in the *Calluna*-heaths resemble in many respects the small bushes in the transition zone between *Calluna*-heath and grass-heath. From these phenomena it thus appeared that the main *Calluna*-heath associations might possibly be degenerating to grass-heath through rabbit attack.

It was thus thought advisable to examine the rabbit dung in the laboratory for traces of fragments of *Calluna* leaves, and with this object in view, fragments of rabbit dung from the transition zone were broken up and boiled alternately in dilute acid and in dilute alkali and filtered off between the boilings, in order to separate out the fibrous portions. The particles which remained after this process were then compared with particles obtained by treating chopped-up *Calluna* leaves in the same way, and after microscopic comparison of the two sets of particles there was no doubt that the rabbit dung contained fragmentary remains of *Calluna* leaves.

Thus it appeared that the rabbits certainly eat the *Calluna* leaves, but whether they eat them to a sufficient extent to cause the main *Calluna*-heath associations to degenerate to grass-heath, except possibly just around the rabbit burrows, remained uncertain. A rabbit-proof cage was erected in the middle of the transition zone, and a great difference between the *Calluna* inside and outside the cage quickly became apparent; the *Calluna* inside the cage recovering from the previous rabbit attack and producing many fresh leaves, while the *Calluna* outside the cage continued to degenerate.

Hence there is no doubt in this case about the *degeneration of Calluna-heath to grass-heath through rabbit attack*. In order to obtain further information about the rapidity of the degeneration, a belt-transect 150 metres long and one metre wide was staked out across a typical area of the degenerating zone, and various means have been adopted for recording the temporary conditions of the *Calluna* bushes at fixed places along this transect at certain dates.

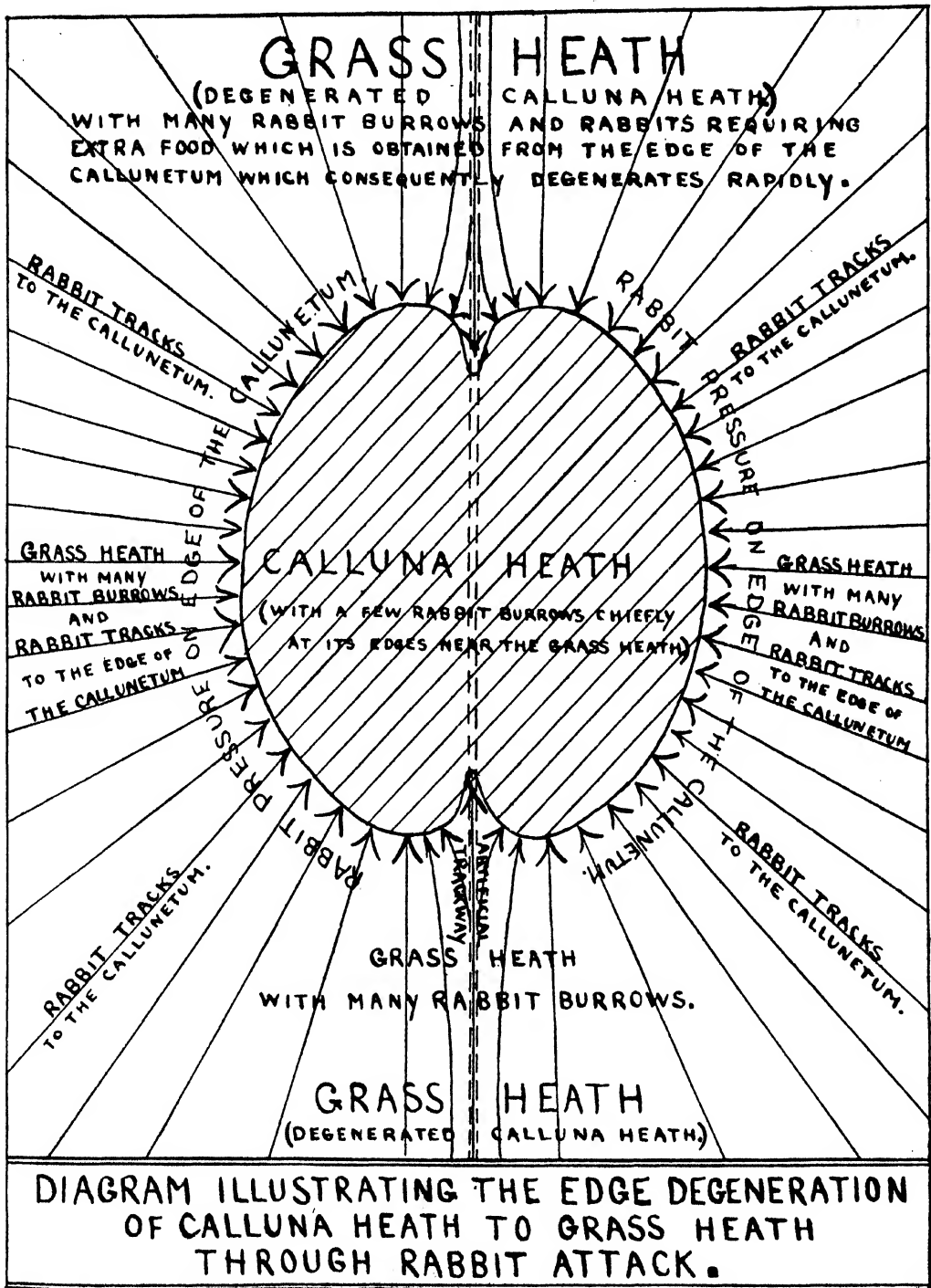


FIG. 6. Degeneration of Grass-Heath. For further explanation see Text.

One of the methods has been to take various orientated photographs¹ at fixed places at intervals (in this case every 20 metres) along the transect. Photos. 3 and 4 (Plate VII) are two of the photographs taken, 20 metres apart, in this way along this transect across the degenerating zone. This long transect across the degenerating zone has also been very carefully charted, the sizes and heights of all the bushes being recorded. The detailed distribution of *Cladonia* along the transect has also been recorded. This chart is on a scale of $\frac{1}{10}$ and is thus 14 metres long and it shows these phenomena in considerable detail. A second transect has also been made across a zone in which the *Calluna* is degenerating very rapidly, and orientated photographs have also been taken along this second transect for the purpose of recording the condition of the bushes at certain positions at certain times. This shorter transect has also been charted on a similar scale to the longer one, and the sizes of the bushes and the distribution of the *Cladonia* on this transect have also been recorded. It is intended to re-chart these transects sometime in the future, in order to see the details of what has happened in the meantime, and the transects will also be re-photographed in exactly the same manner in which they were photographed before, in order that information relating to the details of the degeneration may be derived by comparison of the respective sets of photographs.

It was suggested that a good indication of the amount of rabbit attack to which the vegetation in various places had been subjected might be given by the relative numbers of pellets of rabbit dung per unit area in those places—as this index would tend to integrate the number of rabbits and the time they were present on any given area.

It was realised however that if the integration of the total rabbit attack was to be made over fairly long periods of time a correction might have to be applied to these numbers in order to allow for the decomposition and disintegration of some of the individual dung pellets in those areas which had been occupied by rabbits for a long time. Nevertheless the respective numbers of pellets per unit area might be a good measure of the total rabbit attack at any place during the previous few years.

Unfortunately in fairly exposed positions the rabbit dung pellets are often somewhat blown about by wind and, owing to this, it was only possible to obtain an approximate accuracy of the numbers over fairly large areas, and it was necessary to take small sample areas and estimate the total numbers statistically. But with these precautions comparative numbers were obtained. It was found that the average numbers of rabbit dung pellets per square metre were: at the *Calluna*-heath end of the long transect, 120 ± 23 ; at the middle, 150 ± 37 ; at the grass-heath, 190 ± 46 . These numbers may be taken as representing approximately the relative severities

¹ Farrow, E. P., "On a Photographic Method of Recording Developmental Phases of Vegetation," this JOURNAL, 8, 1915.

of the total rabbit attack at the various places along the transect during a certain period of time. It will be noticed that the total rabbit attack has been greater where the degeneration of the *Calluna* bushes has been greater.

The process of degeneration of *Calluna*-heath to grass-heath owing to rabbit attack is as follows. The attacking rabbits invade the *Calluna* association between the bushes, eventually forming established tracks. They nibble at the *Calluna* leaves which are within reach along the sides of these tracks, and those parts of the bushes which are within reach of the rabbits take on a characteristic rounded form (Plate VIII, Phot. 6). Often, however, the central portions of the bushes are out of reach of the rabbits, and these parts remain tall while only the lower outer portions are rounded off.

The result of this attack is that the once closed *Calluna* association becomes more open in character, and various grasses (chiefly *Agrostis vulgaris* and *Festuca ovina*)—the forerunners of the grass-heath association—appear in the rabbit tracks along with various other plants. At the same time *Cladonia coccifera*, *C. cervicornis*, etc., *Leucobryum glaucum*, *Hypnum schreberi*, *Dicranum scoparium*, etc., which previously formed a subordinate layer of vegetation under and around the once luxuriant *Calluna* bushes, take on a new and enlarged lease of life. The *Cladonia* especially becomes active and grows vigorously amongst the eaten-down branches of *Calluna* (Plate VII, Phot. 4). As the branches of the *Calluna* bushes are eaten down more and more, the *Cladonia* becomes more and more luxuriant, apparently finding a very suitable habitat amongst the eaten-down branches of *Calluna*. The masses of eaten-down *Calluna* branches with *Cladonia* growing densely amongst them retain water very well—like sponges—and are usually very damp during the autumn and winter. Apparently largely owing to this dampness and smothering by the *Cladonia*, the eaten-down *Calluna* branches eventually begin to decay (they are badly decaying in the region shown in Phot. 4), disintegrate, break off at the surface and with the associated *Cladonia* they are eventually blown away, leaving behind the grass-heath association, which has been gradually expanding from the rabbit tracks.

Although the original rabbit-eaten *Calluna* branches which are above the surface of the soil and associated with the damp *Cladonia* decay fairly rapidly, break off at the surface and are blown away along with the associated *Cladonia*; yet the roots of the *Calluna* plants, which are beneath the surface of the soil, and protected from the above mentioned disintegrating agencies, often live on for some time after the destruction of the original subaerial portions, and these protected *Calluna* roots often endeavour to produce fresh subaerial branches. The rabbits however keep these fresh young *Calluna* stems nibbled down close to the surface and in the normal case the protected *Calluna* roots below the surface eventually die and decay.

When first these phenomena were seen, and before their significance was realised, it appeared that the luxuriant *Cladonia* was gradually smothering and killing off the *Calluna* bushes; but apparently the *Cladonia* only does this when associated with rabbit attack on the *Calluna* bushes, and during damp weather in the autumn and winter. It is interesting to note that when the degenerating *Calluna* and the associated luxuriant and formerly smothering *Cladonia* inside the rabbit-proof cage on the transition zone (Phot. 2) were cut off from rabbit attack by the erection of the cage, the *Calluna* in its turn has been able to smother and kill the *Cladonia* which was formerly smothering it.

Often when rabbits attack old *Calluna* bushes, all the lower leaves on the taller branches are eaten off, leaving small and densely crowded clumps of leaves on the extreme ends of the branches; possibly these densely aggregated terminal clumps of leaves give the maximum assimilatory surface while exposing the least leaf surface to the rabbit attack. Only in comparatively few cases is old age the immediate cause of death of the *Calluna* bushes on Cavenham Heath. In the majority of cases the immediate cause of death is rabbit attack either alone or combined with the smothering effect of *Cladonia*.

When the branches of the *Calluna* bushes have been eaten down to a certain extent by rabbits, various other plants besides *Cladonia* often grow amongst these eaten-down *Calluna* branches. *Leucobryum glaucum* is one of the commonest and most deadly of these other injurious associates of the eaten-down branches of rabbit-attacked *Calluna* (Plate VIII, Phot. 5). The *Leucobryum* typically forms a very dense growth, almost like a solid mass of tissue (see Photos. 5 and 6), enclosing many of the eaten-down *Calluna* branches, which are smothered and die and eventually rot away. The winter has also seen *Cladonia* and *Leucobryum* crowding out rabbit-attacked *Calluna* on the north-west Norfolk heaths and also sheep-eaten *Calluna* hummocks on various mountains, and this appears to be a widespread phenomenon. Occasionally other mosses, such as *Dicranum scoparium* and *Hypnum schreberi*, also grow in rabbit-eaten *Calluna* bushes, but these do not usually form dense masses and they do not usually kill parts of the *Calluna* bushes.

The degeneration of *Calluna*-heath to grass-heath primarily owing to rabbit attack is occurring at many places in Breckland and is a widespread phenomenon in this part of England.

In Breckland the degeneration from *Calluna*-heath to grass-heath usually takes place chiefly at the edges of the *Calluna* associations, whereas one might have expected the *Calluna*-heaths to degenerate uniformly all over. The probable explanation is as follows. At first the rabbits live chiefly upon the more luxuriant grass vegetation down the valley sides outside of the *Calluna* associations. Only comparatively few rabbit burrows occur near the centres of the *Calluna*-heaths a long way from the grass-heaths.

Apparently the rabbits greatly prefer grass to heather as their main source of food supply. As the rabbits increase in numbers, however, and become relatively short of food in the valleys, some of them have to migrate from the valleys to the edges of the *Calluna* association on the higher ground for the balance of food supply which they require, and these rabbits tend to make burrows nearer to the edge of the *Calluna* association. There is thus a line of rabbit pressure along the edge of the *Calluna*-heath. If the rabbits are continually increasing in numbers, more and more rabbits are forced to go to the edge of the *Calluna*-heath for the balance of food supply which they require and the rabbit pressure on the edge of the *Calluna*-heath gradually increases and the *edge* of the *Calluna*-heath association gradually retreats. Later additional rabbits tend to make their burrows still further from the valleys near the new edge of the *Calluna* which they are forced to attack owing to the shortage of better food in the valleys. The occupants of the burrows near the *previous* edge of the retreating *Calluna* association also have to go to the *new* edge for their extra food, and the effect of these rabbits is added to that of the occupants of the new burrows near the new edge which thus—if the rabbits are increasing in numbers—continually tends to move more and more rapidly backwards. Also as the central *Calluna*-heath degenerates the total length of its edge decreases in length, and the length of the *Calluna* edge—and consequently the amount of extra food obtainable by a given penetration of the edge—on any given sector of the heath diminishes as the degenerating edge approaches the centre point. In consequence of this the rabbits have to penetrate the degenerating edge more and more in order to obtain a given amount of extra food from the edge and this helps to cause the degenerating edge to move backwards with increasing rapidity.

When the natural enemies of the rabbits are kept down, as they are at Cavenham, the rabbits eventually become extremely numerous and increase almost up to the limit of subsistence. The swarms of rabbits produce a great increase in the number of rabbit burrows on the degenerated grass-heath, and when as at Cavenham the rabbits on the grass-heath have ultimately been cut off from the more rapidly growing vegetation of the valleys by the erection of a rabbit-proof fence around the heath, they are forced to eat down the grass of the grass-heath very closely, and very many of them have to go to the edge of the *Calluna*-heath on the central upper portions for any necessary balance of food supply which they may require. The consequence of all this is that the rabbit pressure all along the line of the *edge* of the *Calluna*-heath at any time continually tends to increase, and the *Calluna*-heath degenerates at its *edge* with continually increasing rapidity.

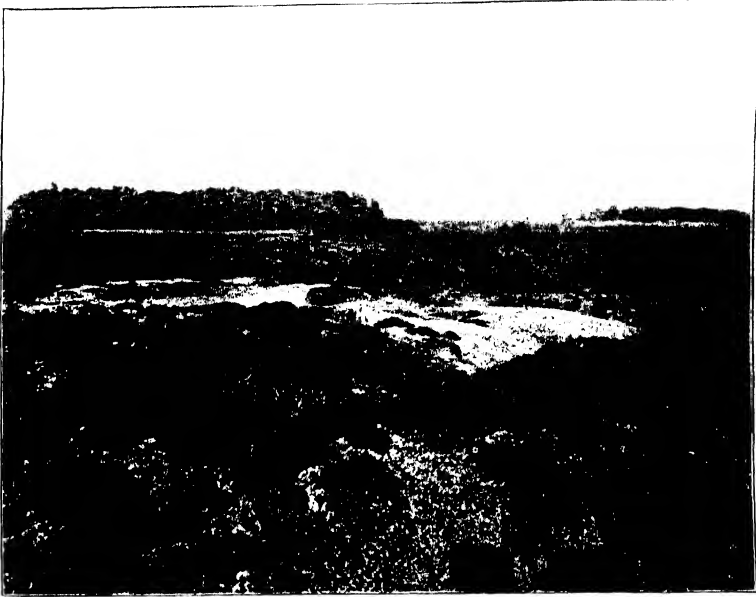
These phenomena are illustrated in Fig. 6.

The fact that *Calluna*-heath usually degenerates sharply at its edges when the degeneration is caused by biotic attack, and the probable reason which

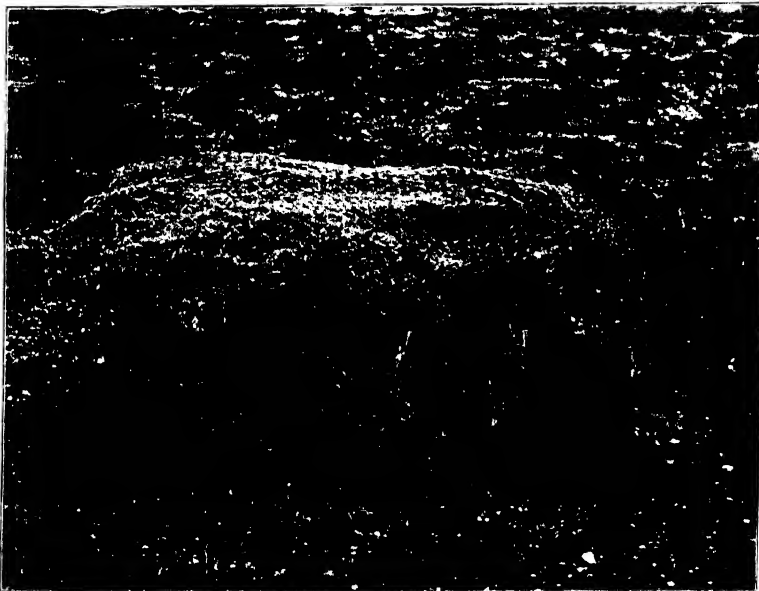
is explained above of such edge degeneration, may also be interesting in view of the fact that many degeneration processes—such as that of oak-birch woodland to heath—usually chiefly occur at the edges of the degenerating association instead of uniformly throughout its area, even although the soil conditions may be fairly uniform throughout its area. In these cases a certain amount of biotic attack is usually present and probably the biotic attack acts upon and produces the edge degeneration of these and other associations in the same way that it causes the edge degeneration of *Calluna*-heath, viz. the necessity of obtaining a balance of extra food from a less palatable kind of plant. The analogy of the edge degeneration in these other classes of cases with the edge degeneration of *Calluna*-heath may rather tend to suggest that these other cases of edge degeneration are very likely chiefly due to some form or other of biotic attack upon the edge of the degenerating association acting in the same way as the biotic attack upon the *Calluna*, and not to such things as leaching of the soil, which if they exist are very likely merely secondary effects of the biotic degeneration.

There is a human trackway across part of Cavenham Heath and the *Calluna* has degenerated to a greater extent at the places where this trackway enters and leaves the *Calluna*-heath. The probable cause of this is that the rabbits from the degenerated area can reach the luxuriant central *Calluna* for their balance of food supply more readily along this trackway than across the ordinary degenerating zone and that the *Calluna* bushes *en route* have incidentally become more eaten down.

It is very interesting to note that on Cavenham Heath and elsewhere the rabbits very severely injure the grass-heath and keep it nibbled down very closely to the surface of the soil, and yet that they enormously benefit it, since if it were not for the rabbits the grass-heath would not exist at all, but would become replaced by heather. The grass-heath owes its very existence to an extremely injurious influence which nevertheless greatly benefits it because it injures its competitor slightly more.



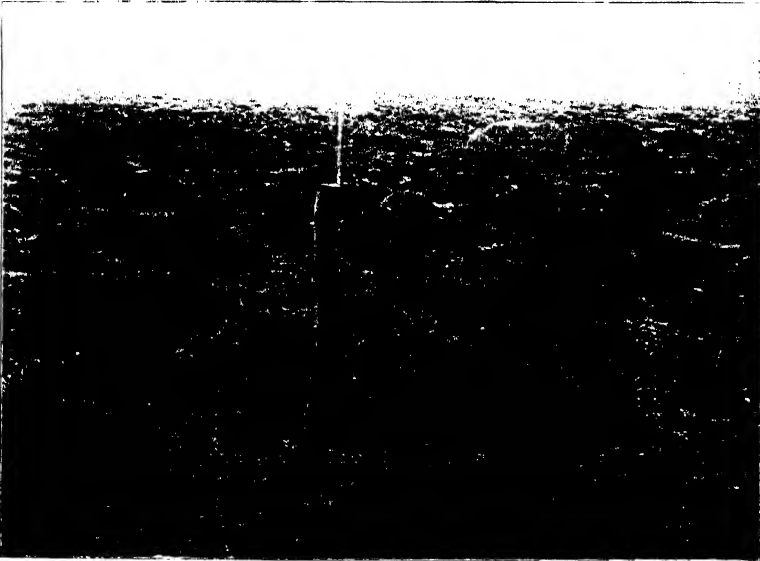
Phot. 1. Bare area and dwarfed *Calluna* bushes around rabbit burrows in *Calluna*-heath. *Cladonia* spp. amongst bushes in foreground (shows whitish in photograph).



Phot. 2. Rabbit-proof cage on degenerating *Calluna* zone, to show difference between the *Calluna* plants inside and outside the cage. The *Calluna* bushes inside the cage possess many leaves and flowers (show whitish), whilst outside the cage the *Calluna* plants are leafless and degenerating--note scraggy leafless bush on the right of the cage and degenerating *Calluna* bushes in the distance.



Phot. 3. Orientated photograph on long transect across the transition zone between *Calluna*-heath and grass-heath where the *Calluna*-heath is degenerating to grass-heath owing to rabbit attack. Note rounded shape of the rabbit-grazed *Calluna* bushes.



Phot. 4. Orientated photograph on the same long transect 20 metres nearer the grass-heath than Phot. 3. The degeneration of the *Calluna*-heath to grass-heath has here proceeded considerably further than in the previous photo. Note the more dwarfed character of the rabbit-grazed *Calluna* bushes. Much *Cladonia* is seen growing amongst the eaten-down *Calluna* branches (shows whitish in the photo). Rabbit tracks are seen in the foreground of the picture.



Phot. 5. Rabbit-attacked *Calluna* bush with the eaten-down *Calluna* branches smothered by a dense growth of *Leucobryum glaucum* (in the centre) and by *Cladonia coccifera* (on the left). The dense growths of *Leucobryum* and *Cladonia* amongst and above the eaten-down *Calluna* branches smother them and cause them to decay.



Phot. 6. Rabbit-grazed and rounded *Calluna* plant with many of the eaten-down branches badly crowded out and smothered by a dense growth of *Leucobryum glaucum*. Rabbit dung pellets and fragments of disintegrated *Calluna* bushes are seen in the foreground on the left.



RELATION OF TRANSPIRATION TO ASSIMILATION IN STEPPE PLANTS

By V. S. ILJIN

INTRODUCTION

During the summer of 1913, thanks to a grant from the Botanical Section of the Petrograd Imperial Society of Naturalists as well as to the kind permission accorded by Professor V. I. Palladin to use the apparatus of the Physiological Section of the Botanical Laboratory in the Petrograd Imperial University, I was enabled to continue my researches on the transpiration of steppe plants and to study in addition their assimilation. The investigations have been made on the virgin steppe reservation in the Countess Panina's estate in the government of Voronezh.

In earlier work on transpiration in steppe plants¹ I tried to show that the simple comparison of the amounts of transpiration of different ecological types of plants cannot give any idea of the extent of their water requirements. The changes of stomata concerned in their reactions to external factors lead to a higher transpiration either of one or of the other species, and it is therefore absolutely hopeless to expect any constant relations in the amounts of transpiration of different plants. We take for example the typical steppe plant *Phlomis pungens*, growing often on very dry and rather insolated places, and compare the amount of its transpiration with (1) that of a meadow type, *Geranium pratense*, (2) that of a plant growing in the meadow steppe, *Senecio doria*, and (3) that of a plant growing in the grass steppe, *Centaurea orientalis*. We are concerned only with cases where the stomata of all the individuals chosen are more or less open. The transpiration of water represented in centigrams per hour per gram of dry weight will be used as a constant unit for comparison.

<i>Phlomis pungens</i>	334	739	374	202	245
<i>Geranium pratense</i>	281	700	399	291	882
Ratio	100 : 82	100 : 95	100 : 107	100 : 144	100 : 360
<i>Phlomis pungens</i>	374	416	210	202	245
<i>Senecio doria</i>	190	291	194	311	395
Ratio	100 : 51	100 : 70	100 : 92	100 : 154	100 : 161
<i>Phlomis pungens</i>	—	241	263	92	188
<i>Centaurea orientalis</i>	—	245	380	153	351
Ratio	—	100 : 102	100 : 145	100 : 166	100 : 187

¹ Iljin, V. S., "Die Regulierung der Spaltöffnungen in Zusammenhang mit der Veränderung des osmotischen Druckes," *Beih. z. bot. Centralbl.* **32**, Abt. 1, 1914, pp. 15-35; "Die Probleme des vergleichenden Studiums der Pflanzentranspiration," *ibid.*, pp. 36-65. Summary in this JOURNAL, **3**, 1915, pp. 170-172, Fig. 25, D-H. Also in *Bull. Imp. Acad. Sci.* (Petrograd), 1913.

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If we examine the ratios above set forth, it will be obvious that they show very striking variations in the plants under comparison, and that any constancy of these ratios is out of the question. As showing that this may be observed in other plants, I shall cite another example:

<i>Stipa capillata</i>	284	387	187	145	115
<i>Caragana frutescens</i>	253	347	245	308	417
Ratio	100 : 89	100 : 90	100 : 131	100 : 212	100 : 362

If however the amount of transpiration does not enable us to judge on the water requirements of different ecological types the question arises as to what should be the criterion for deciding which plants would be better adapted to certain conditions of life when the factor of moisture sinks towards its minimum.

It is necessary to analyse the phenomenon and to ascertain what part transpiration plays in the plant's life and how its lowering will affect the development of the individual.

Different investigators have considered the rôle of transpiration from two standpoints. Most agronomists and physiologists (Helriegel, Zimmermann, Wortmann and others) regard it as important only in the process of passage of mineral salts from roots to leaves. Many among these authors have even postulated strictly quantitative relations between transpiration and amount of salts assimilated. Other investigators, as Hanstein, Reinitzer and especially Haberlandt and Leclerc, are inclined to consider transpiration as an inevitable evil. According to the latter school, the opening of stomata which is necessary for absorbing the carbonic acid from the outside leads incidentally to a loss of water. They mention the luxuriant growth of plants in humid places, as in forcing houses, in woods and swamps, etc., where transpiration is rather low but the process of absorption of carbonic acid by the stomata is fully displayed. Leclerc denies that the transpiration current can play any important part in the passage of salts, since lowering of transpiration would only induce the passage of more concentrated solutions. My object was to study how different protective arrangements developed by the aerial organs may contribute to the growth of plants in dry places poor in water. It is somewhat difficult to see how the arrangements of aerial parts can affect in any way the consumption of mineral salts by the plants, but I shall not dwell on that question, and the present investigation will be limited to the problem of the relation between transpiration and carbon assimilation. Both processes are closely connected with the action of the stomata; it is generally agreed that the rates of water loss and of CO₂ assimilation are directly proportionate to stomatal aperture, and that consequently there exists a close connection between these two processes.

Diminution of transpiration, by inducing the closing of the stomata, will inevitably lead to diminution of assimilation. It would be of great advantage for a plant growing in dry places to avoid losing the possibly

small amount of water keeping the stomata open. This can be achieved with the aid of different protective arrangements such as sinking of the stomata, hairiness, reduction of evaporating surface, etc., which are very characteristic of xerophytes. The latter must show as compared with mesophytes a more economical expenditure of water per unit of absorbed carbonic acid. In physiologico-ecological investigations it is necessary to study transpiration together with assimilation. The relation stated between these two processes should enable us to arrive at conclusions about the comparative adaptability of two or more different species to the given conditions, say, about the better protecting arrangements of one or of the other species.

A question arises as to what unit one should use for comparison in the combined study of transpiration and assimilation—leaf area or dry weight? According to the view set forth above, the protective arrangements contribute, by reducing transpiration, to increased accumulation of organic matter in plants, i.e. the increase of mass. As unit area of leaf of the same mass may have different sizes the mass can be properly measured only by weighing. The following example is mentioned in order to show how different the results may be. The assimilation of three plants with different relations between surface area and dry weight of the leaves has been simultaneously measured. In Table I are given numbers representing the amount of assimilation in c.c. of absorbed CO_2 , the dry weight in grams and the area in sq. cm. of the leaf, the amount per unit area and their ratio.

TABLE I

Species	Dry weight	Surface	Absorbed CO_2 (in c.c.)			Ratio		
			Total	Per gr. of dry weight	Per 1000 sq. cm.	Area to dry weight	Intensity of assimilation	
							Per dry weight unit	Per areal unit
<i>Galeopsis ladanum</i>	0.0203	8.05	0.46	45.03	57.16	397	100	100
<i>Coronilla varia</i>	0.0117	6.17	0.25	21.95	40.50	527	49	71
<i>Phlomis pungens</i>	0.0975	11.55	1.04	21.34	90.00	118	47	157

Looking at the columns showing the intensity of assimilation we can see that calculated per unit of dry weight *Galeopsis ladanum* appeared to show twice as much assimilation as the two other plants. Calculated however per unit of leaf area, *Galeopsis ladanum* assimilated only .75 times as much as *Coronilla varia* and on the other hand 1.5 times more than *Phlomis pungens*. The latter species assimilated four times more actively when calculated per unit area of leaf than in the case of calculation per dry weight (compare columns 4 and 5), *Galeopsis ladanum* only one-fifth as actively, and *Coronilla varia* twice. These figures are striking, as showing how the results can be misrepresented, depending upon the units utilised for calculation. It will be of course a more exact method to estimate the increase of the plant's growth under the influence of external factors by the calculation per dry weight unit, and this method I shall adopt.

METHODS EMPLOYED

Now let us examine the question of the methods of study of transpiration and assimilation.

I have made some observations on plants growing in the soil under natural conditions, but it is difficult to devise satisfactory methods on which one can base exact quantitative calculations of the water lost. The method adopted was to set the plant in a closed vessel and to absorb the water vapour by means of hygroscopic substances. These substances were either placed along with the plant, or an air current was passed through and the outcoming air dried. Both methods are defective in two respects. If one could ensure uniformity in the moisture content of the air in the vessel during

TABLE II

Species	Time			Duration of observation m. s.	Transpiration in cgrm.	
	h.	m.	s.		Absolute	Per hour
<i>Ajuga laxmanni</i> ...	10	12	30			
	10	14	10	1 40	5	200
	10	15	55	1 45	5	189
	10	17	45	1 50	5	171
	10	19	40	1 55	5	157
	10	21	25	1 45	5	189
<i>Phlomis pungens</i> ...	9	56	50			
	10	0	30	3 40	10	164
	10	5	00	4 30	10	134
	10	9	00	4 00	10	150
<i>Clematis integrifolia</i> ...	9	34	30			
	9	37	40	3 10	5	90
	9	40	30	2 40	5	112
	9	43	10	2 50	5	106
<i>Senecio doria</i> ...	10	14	20			
	10	15	55	1 35	5	190
	10	18	10	3 15	10	185
	10	21	15	3 05	10	195
<i>Geranium pratense</i> ...	2	22	45			
	2	24	10	1 25	10	424
	2	25	35	1 25	10	424
	2	28	10	2 25	20	497
<i>Ajuga laxmanni</i> ...	2	36	35			
	2	39	25	2 40	5	113
	2	42	00	2 35	5	116
	2	44	30	2 30	5	120

the experiment, it would be possible to obtain the water vapour actually exhaled by the plants. This however appears impossible; the percentage of moisture in the air varies considerably according to the quantity of hygroscopical substance and the evaporating power of the plants. Also the air draught in the vessel introduces a large amount of moisture which usually precipitates on the walls. Hence the increase shown by this hygroscopic method represents sometimes only half of the weight of water evaporated by the plants, and this is rather strikingly observed in short experiments.

Owing to these and other considerations I was obliged to abandon the attempt to study the transpiration of rooted plants, and fell back on the

method of cutting the plants and determining the amount of evaporation by weighing, although this method is also not quite unimpeachable.

In Table II are shown the results of experiments in which the readings were taken during short periods of time immediately after cutting. All the plants under experiment had widely open stomata.

These figures show that for a few minutes after cutting the rate of transpiration remains fairly constant. There are only to be noticed the characteristic oscillations mentioned in my previous papers. The shorter the time intervals between successive readings, the more noticeable are these oscillations. In Table III are shown the results of readings taken first at short and then at longer intervals.

TABLE III

Species	Time			Duration of observation m. s.	Transpiration in cgrm.	
	h.	m.	s.		Absolute	Per hour
<i>Sanguisorba officinalis</i> ...	9	22	00			
	9	26	30	4 30	10	133
	9	41	00	14 30	34	140
	10	23	30	42 30	48	69
<i>Clematis integrifolia</i> ...	10	9	00			
	10	12	30	3 30	10	171
	10	15	30	3 00	10	200
	10	30	30	15 00	45	180
	11	52	30	82 00	155	114
<i>Senecio doria</i> ...	9	58				
	10	1		3	10	200
	10	6		5	15	180
	10	26		20	55	165
<i>Phlomis pungens</i> ...	10	44	00			
	10	53	30	9 30	18	114
	11	13	30	2 00	45	135
<i>Aristolochia clematitis</i> ...	11	3				
	11	16		13	12	55
	11	56		40	40	60
	12	34		38	42	66
<i>Geranium pratense</i> ...	11	33	00			
	11	41	30	8 30	18	127
	12	00	00	18 30	29	94
	12	36	00	36 00	60	100
<i>Clematis integrifolia</i> ...	10	21				
	10	25		4	5	75
	10	36		11	14	76
	11	10		34	47	73

From these results one can see that the changes in the stomata and the related changes in transpiration rate take place in a fairly gradual way. At any rate for the first 10 to 30 minutes the transpiration rate remains fairly constant, in spite of very great changes in external conditions—in some experiments the plants were transported from a moist habitat to the dry atmosphere of the laboratory.

The determinations of assimilation were made with the aid of gas analysis. The leaves of the plants were placed in a closed vessel, sealed by mercury, and then exposed to light. There arose such methodological questions as, for how long should the experiment proceed, and what amount of water is

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available? Both these factors may affect the state of the stomata and may consequently modify the gas permeability of the leaf, which in my experiments it was important to take into consideration. It is known that excess of CO_2 leads to closing of the stomata, while its absorption might be so rapid that the leaves would not have enough time to decompose it. Therefore the intensity of assimilation would be the same in cases of widely or slightly open stomata. As to the influence of CO_2 on the opening of stomata, 5–7 per cent. may according to Darwin be considered as quite harmless. In my experiments the stomata stood open during one hour or more with 7–9 per cent., though the narrowing of the pore could be observed. My experiments were usually limited in duration to less than one hour, and later even to 20 minutes. The intensity of assimilation was also different when the openings of the stomata varied although the percentage of CO_2 remained high.

Another method tried was the cutting out of equal squares of leaf before and after the experiment and the determination of the increase by weight. This was done in two ways: (1) numerous round discs were cut out of the leaves by a drill before and after the experiment and the increase in dry weight determined; (2) entire leaves were dried and their area measured. But from control experiments it was found that the discs and leaves taken simultaneously not only from different individuals but even from the same plant showed considerable variations of dry weight; the error was 4 to 6 and in some cases even 10 per cent. Particularly large leaves of uniform thickness gave fairly good results, but none of the steppe plants possess such leaves. Narrow leaves, for instance those of grasses, are absolutely unsuitable. After many attempts this method was abandoned.

The methods finally adopted were as follows. Each time there were taken 3 to 5 plants of different ecological types, and their transpiration and assimilation were measured simultaneously. The shoots were cut under water and quickly transferred to a narrow flask filled with water; the plant was then weighed, exposed 10 to 20 minutes under natural conditions, and weighed again. Between the two weighings of the first specimen the other specimens were cut, hence a very small difference in the time of commencing the experiment was in this way obtained for the different plants.

According to their sizes one or several leaves were taken for measurement of the intensity of assimilation. They were placed in a glass tube sealed by mercury with an exactly measured total gas volume and CO_2 percentage. Then the apparatus was exposed to light. After a certain time the leaf was taken out with the aid of a thread tied to the petiole. The error in the determination of CO_2 reached 0.10 to 0.15 per cent.

HABITATS OF THE PLANTS INVESTIGATED

There were several different ecological groups of plants on the portion of the steppe where the observations were made. From south to north in the centre of the area there is a deep ravine at right angles to which there descend smaller ravines. The bottom of these ravines is usually rather wet in consequence of water-flow in spring and after rains. The sides are often abrupt, and of different exposures.

The southern sides, particularly in their upper parts, are covered by typical xerophytes. In the ravines are well sheltered terraces covered with luxuriant meadow plants. Therefore it was possible to obtain representatives of quite different formations. The distribution of plants along the line passing through a small ravine (8.4–12.6 metres deep) running from west to east and having a very abrupt and dry southern side, may be briefly described.

The driest is the top of the southern side—the grass steppe. *Stipa capillata*, *Festuca ovina*, *Koeleria cristata* are there predominant, as well as *Centaurea sibirica*, *Aster villosus*, *Artemisia maritima*, etc., sometimes *Phlomis pungens*, *Salvia nutans* and dwarf specimens of *Caragana frutescens* which grow densely on the northern side opposite. *Stipa capillata* is very rarely found on the upper terrace; among grasses there are predominant *Bromus erectus*, *Koeleria cristata*, *Poa pratensis*, *Festuca ovina*; among dicotyledons *Phlomis pungens*, *Centaurea orientalis*, *Echium rubrum*, *Veronica incana*, *Linum perenne*, *Linum flavum*, etc. In the lower part of the side there are found the plants commonly growing in open but not very dry places (meadow-steppe)—*Senecio doria*, *Centaurea scabiosa*, *Hypericum perforatum*, *Coronilla varia*, *Genista tinctoria*, etc. On the lower terraces there usually grow meadow plants and plants of moist places—*Geranium pratense*, *Sanguisorba officinalis*, *Centaurea jacea*, *Calamagrostis epigeos*, *Thalictrum simplex*, *Lythrum virgatum*, *Lychnis pratensis*, *Alopecurus pratensis*, *Phleum pratense*, *Poa pratensis*, *Betonica officinalis*, *Veronica chamaedrys*. In narrow ravines where a large amount of moisture accumulates the plants grow very luxuriantly, the vegetation including many weeds and representatives of the forest flora—*Aristolochia clematitis*, *Agrimonia eupatorium*, *Melica altissima*, *Nepeta nuda*, *Galeopsis ladanum*, *Galium boreale*, *Galium verum*, *Lathyrus tuberosus*, *Tanacetum vulgare*, etc.

As may be seen from the above description the vegetation is of a diversified character and includes representatives of various ecological groups. We might therefore expect that the water requirements of the different species should be very different, and consequently the amounts of water available should differently affect their processes of life.

RESULTS OF EXPERIMENTS

The chief results of the experiments made are summarised in Table IV, in which are set forth the time of making the experiment, its duration, the conditions of observation, the habitat of the plants, the amounts of transpiration and assimilation which are also quoted per one hour and one gram of dry weight, and lastly the calculation of the quantity in grams of water lost by the plant under experiment per c.c. of CO_2 decomposed. Other results from these experiments will be cited as occasion arises. I should like to point out that only the results of the same experiment are comparable as only in this case were all conditions such as CO_2 percentage, intensity of illumination, temperature, moisture, etc., kept uniform.

The methods I have used are of course not exact and may be open to question. But it may perhaps be considered as some proof of their relative accuracy that 15 experiments have given quite the same results and, moreover, they perfectly agree with the observations made on the distribution of the plants.

From the data set forth in Table IV we may draw the following conclusions.

(1) Plants growing in dry places are adapted to a more economical consumption of water. Their protective arrangements enable them to lose less water per unit of decomposed carbonic acid. Let us compare how much water per c.c. of decomposed carbonic acid is lost by xerophytes and mesophytes under similar conditions.

Of the species used in Experiment 2, *Phlomis pungens* grows on the grass steppe and *Betonica officinalis* on slight declivities where water is streaming in time of heavy rains or during the spring melting. The amount of water at the disposal of *Betonica* is probably larger, but the external conditions of evaporation are about equal for both. *Betonica* lost 31.4 cgr. of water per c.c. of CO_2 decomposed, whilst *Phlomis* lost 14 cgr., i.e., in the ratio 100:45. In another experiment (9) made during the earlier hours of the day the transpiration of *Betonica* was 121.2 cgr. and that of *Phlomis* 84 cgr., in the ratio 100:69.

Experiment 3 deals with the typical grass steppe plants, *Stipa capillata*, *Caragana frutescens* and *Phlomis pungens*, as well as *Coronilla varia* growing on the slope marked by the appearance of mesophytes, this being the limit of *Coronilla varia* distribution. The amount of water (in centigrams) lost per c.c. of CO_2 decomposed and the ratio between them are as follows:

	Evaporation	Ratio
<i>Coronilla varia</i>	237.5	100
<i>Caragana frutescens</i>	72.4	30
<i>Phlomis pungens</i>	68.2	22
<i>Stipa capillata</i>	39.9	16

The more typical xerophytes show a more economical water expenditure.

In Experiment 4 the conditions of observation were exactly like those of Experiment 3. *Coronilla varia* evaporated 1176 cgr. of water per c.c. of CO₂ decomposed; *Stipa capillata* 160 cgr.; the ratio is 100 : 14.

In Experiment 8 on the grass steppe, *Phlomis pungens* lost 12.25 cgr. of water, *Amygdalus nana* 53.92, and *Centaurea orientalis* 42.7. The ratio is 23 : 100 : 79

In Experiments 13 and 14 we have a comparison of the transpiration and assimilation of *Phlomis pungens* and *Senecio doria* growing on the meadow steppe. It is to be pointed out that they did not grow together, *Phlomis pungens* occurring on slight elevations and *Senecio doria* in lower places. Experiment 13 was made later (after 1 p.m.) than Experiment 14 (about 11 a.m.), and the contrasts are more apparent, because of the less drought-resistant plants suffering more of the heat of the day. In Experiment 13 *Phlomis pungens* lost 34.5 cgr. of water per c.c. of CO₂ decomposed, *Senecio doria* 414.7 cgr.; the ratio is 8 : 100. In Experiment 14 *Phlomis pungens* lost 37.2 cgr. and *Senecio doria* 184.5 cgr.; the ratio is 21 : 100.

Experiments 1 and 10 give the ratios for *Aristolochia clematitis* and for steppe plants. *Aristolochia clematitis* of course did not grow together with the latter, but could be found on the hill at about five paces distance from the ravine, whilst the prairie plants were found 5 to 7 m. higher. The individuals of *Aristolochia* on the limit of its distribution were dwarf ones. In Experiment 10 *Aristolochia clematitis* lost 544 cgr. of water per c.c. of CO₂, *Stipa capillata* only 125; the ratio is 100 : 23.

It must be pointed out that in no case was the water loss in xerophytes per unit of decomposed CO₂ found to be equal to or more than that in mesophytes.

(2) As the mesophytes evaporate water in a very uneconomical way they must close their stomata in dry places in order to reduce evaporation, thus also diminishing the rate of assimilation as well, whereas in the case of xerophytes, which are adapted to extreme conditions of existence, assimilation in similar circumstances proceeds actively.

In order to show how great the contrasts may be, let us take first the figures illustrating the normal assimilation of plants in their natural conditions. It may be generally taken as a rule that the assimilation of mesophytes proceeds more rapidly than that of xerophytes, probably owing to (1) their more developed light absorbing surface, (2) the better permeability of their covering tissues.

In Experiment 5 it was found that at about 9 a.m., when all was covered with dew and the opening of stomata was at its maximum, the assimilation of *Galeopsis ladanum* grown in the wet hollow was equal to 45 c.c. of decomposed CO₂ and that of *Phlomis pungens* only 21 c.c. In Experiment 9 the assimilation of *Betonica officinalis* on the damp meadow was 16.46 c.c. of

TABLE IV.

Species	Place		Dry weight		Transpiration in cgr.			Decomposed CO ₂		Transpiration in cgr. of water per c.c. of CO ₂ decomposed
	of habitat	of experiment	During assimilation	During transpiration	Duration of observation in minutes	Absolutely	Per hour of dry weight	Absolutely	Per hour of dry weight	
Experiment 1. 30th June. Transpiration from 1.13 p.m. till 1.39 p.m. in the day. Assimilation for 40 minutes with 6 % of CO ₂ .										
1	Aristolochia clematidis	Ravine	0.059	1.465	18	21	48	0.167	4.25	11
2	Aristolochia clematidis	Grass steppe	0.059	0.745	10	90	1498	0.167	4.25	171
3	Aristolochia clematidis	"	0.055	0.470	15	47	400	0	0	∞
4	Centaurea orientalis...	"	0.060	0.685	13	53	351	0.252	6.25	56
Experiment 2. 2nd July. Transpiration from 12.23 p.m. till 1.5 p.m. Assimilation for 40 minutes with 4.85 % of CO ₂ .										
5	Phlomis pungens	Grass steppe	0.0980	0.8150	6	7.5	92	0.482	6.56	14.0
6	Betonica officinalis	"	0.0775	0.5500	5	10	218	0.536	6.94	31.4
7	Clematis integrifolia...	"	0.0514	1.0900	5	12	133	0.340	7.49	17.8
Experiment 3. 5th July. Transpiration from 1.27 p.m. till 1.56 p.m. Assimilation for 40 minutes with 4.91 % of CO ₂ .										
8	Stipa capillata	Grass steppe	0.125	1.150	12	43	187	0.488	4.69	39.9
9	Phlomis pungens	"	0.125	0.875	12.5	53	279	0.526	4.09	68.2
10	Caragana frutescens	"	0.073	0.755	12	37	245	0.206	3.38	72.4
11	Coronilla varia	"	0.157	0.485	11	49	551	0.364	2.32	237.5
Experiment 4. Transpiration from 11.6 p.m. till 11.32 a.m. Assimilation for 40 minutes with 4.72 % of CO₂.										
12	Coronilla varia	Ravine	0.0254	0.195	12	43.5	1115	0.336	26.5	421
13	Coronilla varia	Grass steppe	0.0254	0.270	12	31.5	584	0.336	26.5	220
14	Coronilla varia	Grass steppe	0.0301	0.350	12	33.5	764	0.130	6.5	1176
15	Stipa capillata	"	0.0122	0.620	12	60.3	458	0.250	28.7	160
Experiment 5. 8th July. Transpiration from 8.44 a.m. till 10.5 a.m. Assimilation for 30 minutes with 7.45 % of CO ₂ .										
16	Galeopsis ladanum	Ravine	0.0203	0.273	14	11	173	0.46	45.03	3.8
17	Phlomis pungens	Grass steppe	0.0975	0.975	12	72	318	1.04	21.34	10.1
18	Galeopsis ladanum	Ravine	0.0203	0.260	7	51	1681	0.46	45.03	37.3
Experiment 6. 11th July. Transpiration from 10.31 a.m. till 11.55 a.m. Assimilation for 30 minutes with 2.75 % of CO ₂ .										
19	Caragana frutescens...	Grass steppe	0.0890	1.4143	13	98	417	0.202	4.54	91.8
20	Phlomis pungens	"	0.0556	1.7141	12.5	138	387	0.476	17.13	22.6
21	Stipa capillata	"	0.1136	0.9795	13	24.5	115	0.548	9.64	11.9
Experiment 7. 15th July. Transpiration from 9.45 a.m. till 10.16 a.m. Assimilation for 25 minutes with 3.57 % of CO ₂ .										
22	Stipa capillata	Grass steppe	0.0639	0.5560	21	32	163	0.230	8.64	18.9
23	Phlomis pungens	"	0.1293	3.1615	15	200	253	0.606	11.24	22.3
24	Centaurea orientalis...	"	0.1236	0.9078	20	68	225	0.410	7.96	28.3
Experiment 8. 17th July. Transpiration from 8.40 a.m. till 9.20 a.m. Assimilation for 25 minutes with 7.71 % of CO ₂ .										
25	Phlomis pungens	Grass steppe	0.1041	3.1020	15	140	184	0.652	15.01	12.3
26	Caragana frutescens	"	0.1025	1.3509	15	53	156	0.342	7.93	19.7
27	Amygdalus nana	"	0.1084	2.1528	12	65	151	0.126	2.80	53.9
28	Centaurea orientalis...	"	0.1644	1.0687	16	45	253	0.406	5.92	42.7

Experiment 9. 17th July. Transpiration from 11.3 a.m. till 12.26 p.m. Assimilation for 25 minutes with 6.26 % of CO ₂ .									
29 <i>Betonica officinalis</i> ...	Meadow steppe	0.0982	0.2933	12	40	682	0.228	5.63	121
30 <i>Phlomis pungens</i> ...	Grass steppe	0.0730	2.1745	12	183	420	0.152	5.00	84
31 <i>Centaurea orientalis</i> ...	"	0.1140	0.4643	12	30	323	0.138	9.92	110
32 <i>Betonica officinalis</i> ...	Meadow	0.0420	0.5346	12	85	159	0.228	16.46	10
Experiment 10. 19th July. Transpiration from 12.36 p.m. till 12.59 p.m. Assimilation for 30 minutes with 5.50 % of CO ₂ .									
33 <i>Stipa capillata</i> ...	Grass steppe	0.1068	0.5120	10	33	387	0.110	3.09	125
34 <i>Aristolochia clematidis</i> ...	Meadow steppe	0.0915	0.4820	16	113	963	0.054	1.77	544
35 <i>Aristolochia clematidis</i> ...	Ravine	0.0918	0.9870	20	39	119	0.154	5.03	24
Experiment 11. 21st July. Transpiration from 12.10 p.m. till 1.33 p.m. Assimilation for 20 minutes with 3.26 % of CO ₂ .									
36 <i>Geranium pratense</i> ...	Meadow	0.0274	1.1368	30	98	158	0.224	24.54	6.5
37 <i>Sanguisorba officinalis</i> ...	"	0.0619	1.1022	20	38	103	0.140	6.78	15.2
38 <i>Trifolium medium</i> ...	"	0.0572	1.3076	30	81	124	0.222	11.64	10.7
39 <i>Stipa capillata</i> ...	Grass steppe	0.0880	0.8731	10	20	137	0.232	7.91	18.5
40 <i>Centaurea sibirica</i> ...	"	0.0923	0.6066	10	47	465	0.242	7.87	59.2
Experiment 12. 24th July. Transpiration from 1.13 p.m. till 1.52 p.m. Assimilation for 20 minutes with 1.20 % of CO ₂ .									
41 <i>Senecio doria</i> ...	Meadow steppe	0.1127	1.9000	20	198	313	0.150	3.99	78.5
42 <i>Geranium pratense</i> ...	Meadow	0.0502	0.7469	25	95	308	0.170	10.16	30.3
43 <i>Caragana frutescens</i> ...	Grass steppe	0.0841	2.1794	10	139	383	0.110	3.92	97.7
44 <i>Stipa capillata</i> ...	"	0.0730	0.4757	12	27	284	0.127	5.22	54.4
45 <i>Centaurea sibirica</i> ...	"	0.0932	1.8633	12	125	335	0.162	5.22	64.2
46 <i>Senecio doria</i> ...	Meadow steppe	0.1127	2.0332	10	209	617	0.150	3.99	154.6
47 <i>Geranium pratense</i> ...	Meadow	0.0502	1.2142	10	246	1216	0.170	10.16	119.7
Experiment 13. 30th July. Transpiration from 1.6 p.m. till 1.32 p.m. Assimilation for 20 minutes with 2.98 % of CO ₂ .									
48 <i>Phlomis pungens</i> ...	Meadow steppe	0.0563	2.9729	20	200	202	0.110	5.86	34.5
49 <i>Senecio doria</i> ...	"	0.1038	3.5393	18	330	311	0.026	0.75	414.7
50 <i>Senecio doria</i> ...	Ravine	0.0901	1.8975	18	127	223	0.162	5.39	41.4
51 <i>Geranium pratense</i> ...	"	—	1.0763	17	89	291	0	0	∞
Experiment 14. 2nd August. Transpiration from 11.46 a.m. till 12.40 p.m. Assimilation for 20 minutes with 6.14 % of CO ₂ .									
52 <i>Phlomis pungens</i> ...	Meadow steppe	0.0919	3.3848	10	155	245	0.20	6.60	37.2
53 <i>Senecio doria</i> ...	"	0.1821	3.8763	10	255	395	0.13	2.14	184.5
54 <i>Senecio doria</i> ...	Ravine	0.0800	0.8439	17	25	223	0.47	14.71	15.2
55 <i>Geranium pratense</i> ...	"	0.0963	0.3199	18	220	365	—	0.21	∞
Experiment 15. 4th August. Transpiration from 12.50 p.m. till 1.23 p.m. Assimilation for 20 minutes with 6.33 % of CO ₂ .									
56 <i>Stipa capillata</i> ...	Grass steppe	0.0883	0.4074	15	20	196	0.178	6.05	32.4
57 <i>Caragana frutescens</i> ...	Growing thick	0.0617	2.2188	18	95	233	0.122	5.93	39.3
58 <i>Caragana frutescens</i> ...	Grass steppe	0.0551	1.3452	11	100	248	0.014	0.76	326.0

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CO₂ and that of *Phlomis pungens* in the prairie 5.00 c.c. In Experiment 11 on a wet dull day *Geranium pratense* assimilated 24.54 c.c., *Stipa capillata* 7.91, and *Phlomis pungens* 7.87. In Experiment 14 *Senecio doria* decomposed 14.71 c.c. of CO₂ and *Phlomis pungens* only 6.60.

Let us now see how assimilation proceeds in mesophytes in dry places.

In Experiment 9 has been determined the assimilation of *Betonica officinalis*. There were taken two specimens, one from the meadow steppe developed under hard conditions of life and the other from the meadow where it thrived quite luxuriantly. The assimilation of the first specimen was 5.63 c.c. of CO₂ and that of the second 16.46 c.c. We observe here an apparent reduction.

In Experiment 3 there are compared plants grown on the side of a hill with south-west exposure. Its upper zones were covered with xerophytes; *Coronilla varia* grew to about the middle of the hill. The assimilation of *Stipa capillata* was 4.69 c.c. of CO₂, that of *Phlomis pungens* 4.09 c.c., that of *Caragana frutescens* 3.38 and that of *Coronilla varia* only 2.32 c.c. In this experiment we observe the reduction of the latter plant.

In Experiments 1 and 10 the assimilation of *Aristolochia clematitis* has been determined. It was grown (1) in its normal conditions in a wet hollow among high grasses and (2) on the edge of its distribution near the bottom of the hill where there were found only dwarf specimens. In Experiment 10 the assimilation of the normal specimen was 5.03, that of the dwarf form only 1.77, and that of *Stipa capillata* on the hill 3.09. Here is clearly seen the reduction not only in comparison with plants under natural conditions but also in comparison with xerophytes.

TABLE V

Species	Habitat	Experiment 13	Experiment 14
<i>Phlomis pungens</i>	Steppe	5.86	6.60
<i>Senecio doria</i>	"	0.75	2.14
<i>Senecio doria</i>	Ravine	5.39	14.71
<i>Geranium pratense</i>	"	0	0

Quite an analogous phenomenon is to be observed in Experiments 13 and 14 for *Geranium pratense* and *Senecio doria*. On flat meadow steppe situated in lower parts and sheltered by parallel hills there grew *Senecio doria*, and on slight elevation *Phlomis pungens*. There was passing a shallow ravine where there was running rain water, and *Senecio doria* and *Geranium pratense* were found here. The latter was under the severest conditions of existence, and no assimilation could be noticed, this being probably due to the hot weather in July. On the meadow, however, under more favourable conditions, its assimilation was fully displayed. In these two experiments the numbers although different in their quantitative sense lead to similar results. The difference is due to the fact that Experiment 14 was made

in earlier hours of the day, hence their assimilation was higher. As shown in Table V, the assimilation of *Senecio doria* on the steppe was less than (1) in the ravine and (2) that of *Phlomis pungens* which is a xerophyte.

(3) In consequence of the greater amount of moisture in the environment, mesophytes lose, under normal conditions, less water and the rate of transpiration is often slower than that of xerophytes. If, however, the mesophytes having the same rate of assimilation were transferred to the dry places in which the xerophytes grow, their transpiration would increase to a greater extent. In further experiments there was determined the transpiration (1) of xerophytes in their normal conditions, (2) of mesophytes in their natural environment, (3) of specimens of mesophytic species which were cut and exposed to the same conditions of life as xerophytes.

Table VI shows the results of experiments where the determinations of assimilation and transpiration were made in the natural habitats of xerophytes and mesophytes.

TABLE VI

Species	Habitat	Transpiration in cgr. per hour per gr. of dry weight	Assimilation in c.c. per hour per gr. of dry weight	Transpiration in cgr. of water per c.c. of decom- posed CO ₂
<i>Experiment 9</i>				
32 <i>Betonica officinalis</i>	Meadow	159	16.46	9.9
30 <i>Phlomis pungens</i>	Steppe	420	5.00	84.0
<i>Experiment 10</i>				
36 <i>Geranium pratense</i>	Meadow	158	24.54	6.5
38 <i>Trifolium montanum</i>	"	124	11.64	10.7
39 <i>Stipa capillata</i>	Steppe	137	7.91	18.5
40 <i>Centaurea sibirica</i>	"	465	7.87	59.2
<i>Experiment 13</i>				
50 <i>Senecio doria</i>	Ravine	202	5.39	41.4
48 <i>Phlomis pungens</i>	Steppe	223	5.86	34.5
<i>Experiment 14</i>				
54 <i>Senecio doria</i>	Ravine	223	14.71	15.2
52 <i>Phlomis pungens</i>	Steppe	245	6.60	37.2

As can be seen from the above table the absolute amount of transpiration of mesophytes is either like that of xerophytes or even lower. The same can be said with reference to the loss of water per unit of CO₂ decomposed.

Let us observe now how these quantities will vary if the mesophytes are transferred to the habitats of xerophytes.

Table VII shows that in this case the absolute quantity of transpiration as well as its relation to assimilation will considerably increase. *Senecio doria* on being transferred from meadow steppe to grass steppe doubled its transpiration and lost three times more water per unit of CO₂ decomposed than the xerophytes. Quite a similar result was obtained with *Cypripedium varia*. Still more striking results are given by the plants of meadow and meadow steppe; *Geranium pratense* on being transferred increased its transpiration three times, *Galeopsis ladanum* almost ten times, *Aristolochia*

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clematitis about 31 times. If we compare the loss of water per unit of CO₂ decomposed in these plants and in xerophytes we shall find that the former have lost much more water than the latter.

Thus plants living usually under quite different conditions of moisture show different water requirements—xerophytes spend water more economically.

TABLE VII

	Species	Habitat	Place of determination of transpiration	Transpiration in cgr. per hour per gr. of dry weight	Assimilation per hour per gr. of dry weight	Transpiration in cgr. per c.c. of decomposed CO ₂
<i>Experiment 1</i>						
1	<i>Aristolochia clematitis</i>	Ravine	Ravine	48	4.25	11
2	<i>Aristolochia clematitis</i>	"	Steppe	1492	4.25	351
3	<i>Centaurea orientalis</i> ...	Steppe	"	35	6.26	56
<i>Experiment 4</i>						
13	<i>Coronilla varia</i> ...	Meadow st.	Meadow st.	584	2.65	220
12	<i>Coronilla varia</i> ...	"	Grass st.	1115	2.65	421
15	<i>Stipa capillata</i> ...	Grass st.	"	458	2.87	160
<i>Experiment 5</i>						
16	<i>Galeopsis ladanum</i> ...	Ravine	Ravine	173	45.03	3.8
18	<i>Galeopsis ladanum</i> ...	"	Steppe	1681	45.03	37.3
17	<i>Phlomis pungens</i> ...	Steppe	"	318	21.34	14.9
<i>Experiment 12</i>						
42	<i>Geranium pratense</i> ...	Meadow	Meadow	308	10.16	30.3
97	<i>Geranium pratense</i> ...	"	Grass st.	1216	10.16	119.7
41	<i>Senecio doria</i> ...	Meadow st.	Meadow st.	313	3.99	78.5
46	<i>Senecio doria</i> ...	"	Grass st.	617	3.99	154.6
44	<i>Stipa capillata</i> ...	Grass st.	"	284	5.22	54.4
45	<i>Centaurea sibirica</i> ...	"	"	335	5.22	64.2

The following types, with their typical representatives, may be distinguished. (1) Ravine, with *Aristolochia clematitis* and *Galeopsis ladanum*. (2) Meadow, with *Geranium pratense*, *Trifolium montanum* and *Betonica officinalis*. (3) Meadow steppe, with *Senecio doria* and *Coronilla varia*. (4) Grass steppe, with *Centaurea orientalis*, *Amygdalus nana*, *Caragana frutescens*, *Phlomis pungens*, *Stipa capillata* and *Centaurea sibirica*, the latter in drier places.

The water requirement will be different not only for different groups but also for different representatives of the same group. The more drought-resistant the plant, the more economical its expenditure of water.

In order to determine the comparative drought-resistance it would be desirable to place the plants under experiment in identical conditions. But it is of course out of the question to find plants of quite different types growing in quite similar conditions of the natural habitat. Therefore in order to examine the plants with large water requirements I have taken them (1) in their typical habitat and (2) on the edge of their distribution where they begin to suffer from excessive drought. Below I give tables for the plants in the ravine and from the steppe. The former have been taken (1) in the

ravine, the determination of transpiration being made on the spot, (2) by cutting and transferring individuals grown in the ravine on to the steppe in order to determine the transpiration, and (3) by finding an individual on the edge of its distribution.

TABLE VIII

Species	Habitat	Place of determination of transpiration	Transpiration in cgr. per hour per gr. of dry weight	Assimilation in c.c. per hour per gr. of dry weight	Transpiration in cgr. per c.c. of decomposed CO ₂
<i>Experiment 1</i>					
1 <i>Aristolochia clematitis</i>	Ravine	Ravine	48	4.25	11
2 <i>Aristolochia clematitis</i>	"	Steppe	1492	4.25	171
3 <i>Aristolochia clematitis</i>	Steppe	"	400	0	∞
4 <i>Centaurea orientalis</i> ...	"	"	351	6.26	56
<i>Experiment 10</i>					
33 <i>Stipa capillata</i> ...	Steppe	Steppe	387	3.09	125
34 <i>Aristolochia clematitis</i>	"	"	963	1.77	544
35 <i>Aristolochia clematitis</i>	Ravine	Ravine	119	5.03	24
<i>Experiment 5</i>					
16 <i>Galeopsis ladanum</i> ...	Ravine	Ravine	173	45.03	4
17 <i>Phlomis pungens</i> ...	Steppe	Steppe	318	21.34	15
18 <i>Galeopsis ladanum</i> ...	Ravine	"	1681	45.03	37

As shown in Table VIII, ravine plants on being transferred to the habitat of steppe plants show a great increase in transpiration, and lose not only very large amounts of water—as for instance *Aristolochia clematitis* 1492 cgr. and *Galeopsis ladanum* 1681 cgr., whilst the steppe plants are losing on the average 300–400 cgr.—but also a very heavy water loss per unit of decomposed carbonic acid, their loss of water being much greater than that of steppe plants.

TABLE IX

Species	Habitat	Place of determination of transpiration	Transpiration in cgr. per hour per gr. of dry weight	Assimilation in c.c. per hour per gr. of dry weight	Transpiration in cgr. per c.c. of decomposed CO ₂
<i>Experiment 12</i>					
41 <i>Geranium pratense</i> ...	Meadow	Meadow	308	10.16	30
46 <i>Geranium pratense</i> ...	"	Grass st.	1216	10.16	120
43 <i>Stipa capillata</i> ...	Grass st.	"	284	5.22	54
<i>Experiment 13</i>					
48 <i>Senecio doria</i> ...	Ravine	Ravine	223	539	41
49 <i>Geranium pratense</i> ...	"	"	291	0	
<i>Experiment 14</i>					
53 <i>Senecio doria</i> ...	Ravine	Ravine	223	14.71	15
54 <i>Geranium pratense</i> ...	"	"	365	— 0.21	
<i>Experiment 11</i>					
36 <i>Geranium pratense</i> ...	Meadow	Meadow	158	24.54	7
37 <i>Trifolium montanum</i>	"	"	124	11.64	11
38 <i>Stipa capillata</i> ...	Grass st.	Grass st.	137	7.91	19
<i>Experiment 2</i>					
5 <i>Phlomis pungens</i> ...	Grass st.	Meadow	92	6.56	14
6 <i>Betonica officinalis</i> ...	Meadow st.	Grass st.	218	6.94	31
<i>Experiment 9</i>					
29 <i>Betonica officinalis</i> ...	Meadow st.	—	682	5.63	121
32 <i>Betonica officinalis</i> ...	Meadow	—	159	16.46	84
30 <i>Phlomis pungens</i> ...	Grass st.	—	420	5.00	10

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The figures in Table IX show that the meadow plants assimilate more rapidly in their natural conditions. To this may be attributed the luxuriant growth of meadow grasses, which are even able, under favourable conditions, to kill the xerophytes. *Geranium pratense* on the meadow nearly reached a man's height and its leaves had a diameter of 10 to 15 cm. A noticeable decrease of assimilation is observed as soon as the meadow grasses are transferred to dry places. In Experiment 9 *Betonica officinalis* on the meadow assimilated 16.46 c.c. of CO₂ and on the steppe, or rather on a slight declivity, only 5.63, i.e. about one-third as much. In Experiments 13 and 14 *Geranium pratense* growing together with *Senecio doria* did not assimilate at all, whilst *Senecio doria* showed active assimilation.

The transpiration of the meadow species even in their native habitats is more active than that of the steppe species. The transference affects it in a particularly striking way. The amount of water lost per unit of decomposed carbonic acid is also considerable.

TABLE X

Species	Habitat	Place of observation	Transpiration in cgr. per hour per gr. of dry weight	Assimilation in c.c. per hour per gr. of dry weight	Transpiration in cgr. per c.c. of decomposed CO ₂
<i>Experiment 3</i>					
8 <i>Stipa capillata</i>	...	Grass steppe	187	4.69	40
9 <i>Phlomis pungens</i>	...	"	279	4.09	68
11 <i>Coronilla varia</i>	...	The limit of grass steppe	551	2.32	238
<i>Experiment 4</i>					
12 <i>Coronilla varia</i>	...	Meadow st.	584	2.65	221
13 <i>Coronilla varia</i>	...	"	1115	2.65	420
14 <i>Coronilla varia</i>	...	Limit of gr. st.	764	0.65	1176
15 <i>Stipa capillata</i>	...	Grass st.	458	2.87	160
<i>Experiment 12</i>					
40 <i>Senecio doria</i>	...	Meadow st.	313	3.99	79
46 <i>Senecio doria</i>	...	"	617	3.99	155
44 <i>Centaurea sibirica</i>	...	Grass st.	335	5.22	64
<i>Experiment 13</i>					
47 <i>Phlomis pungens</i>	...	Meadow st.	202	5.86	35
48 <i>Senecio doria</i>	...	"	311	0.75	415
49 <i>Senecio doria</i>	...	Ravine	223	5.39	41

Now we consider the plants of meadow steppe. From Table X we see that the rate of assimilation decreases when the plants are transferred to dry places, while that of transpiration increases very considerably in comparison with xerophytes, a marked increase after transference and less economical water expenditure per unit of decomposed CO₂. It is interesting to point out that the meadow steppe plants when transferred to steppe only double their rate of transpiration, whilst the plants of meadows and ravines increase it four and even (Exps. 16 and 18) ten and (Exps. 1 and 2) 31 times.

Now let us examine the different representatives of grass steppe (Table XI).

The observations on the distribution of the species lead us to the conclusion that the most drought-resistant is *Stipa capillata*, then *Centaurea sibirica*, *Caragana frutescens* and *Phlomis pungens*; the two latter however are rarely found on the dry places. *Centaurea orientalis* is never found on elevations and bare places, it grows beyond the line of Stipetum distribution. As far as the assimilation is concerned it is interesting to note that *Phlomis pungens* has especially luxuriant foliage and that only in one experiment (Exp. 6) out of five was its assimilation found to be less than that of *Stipa capillata* which was due to a rather dry place; also that *Caragana frutescens* (Exp. 15) when found as dwarf specimens assimilated eight times less than when found among the dense growth of the Stipetum—the same is to be seen in Experiment 12, though in a less striking degree.

TABLE XI

Species	Habitat	Transpiration in cgr. per hour per gr. of dry weight	Assimilation in c.c. per hour per gr. of dry weight	Transpiration in cgr. per c.c. of de- composed CO ₂
<i>Experiment 3</i>				
8 <i>Stipa capillata</i> ...	Steppe	187	4.69	40
9 <i>Phlomis pungens</i> ...	„	279	4.09	68
<i>Experiment 6</i>				
19 <i>Caragana frutescens</i>	Steppe	417	4.54	92
20 <i>Phlomis pungens</i> ...	„	387	17.13	23
21 <i>Stipa capillata</i> ...	„	115	9.64	12
<i>Experiment 7</i>				
22 <i>Stipa capillata</i> ...	Steppe	163	8.64	19
23 <i>Phlomis pungens</i> ...	„	253	11.24	22
24 <i>Centaurea orientalis</i>	„	225	7.96	28
<i>Experiment 8</i>				
25 <i>Phlomis pungens</i> ...	Steppe	184	15.01	12
26 <i>Caragana frutescens</i>	„	156	7.93	20
27 <i>Amygdalus nana</i> ...	„	151	2.80	54
28 <i>Centaurea orientalis</i>	„	253	5.92	43
<i>Experiment 9</i>				
30 <i>Phlomis pungens</i> ...	Steppe	420	5.00	84
31 <i>Centaurea sibirica</i> ...	„	323	2.92	110
<i>Experiment 11</i>				
39 <i>Stipa capillata</i> ...	Steppe	137	7.91	19
40 <i>Centaurea sibirica</i> ...	„	465	7.87	59
<i>Experiment 12</i>				
42 <i>Caragana frutescens</i>	Steppe	383	3.92	98
43 <i>Stipa capillata</i> ...	„	284	5.22	54
44 <i>Centaurea sibirica</i> ...	„	335	5.22	64
<i>Experiment 15</i>				
55 <i>Stipa capillata</i> ...	Steppe	196	6.05	32
56 <i>Caragana frutescens</i>	„	248	0.76	326
57 <i>Caragana frutescens</i>	Dense growth	233	5.93	39

It should be noted that the relation of assimilation to transpiration in different species is of importance only when the moisture is at its minimum. In meadow, wood or swamp, and generally in places with an abundant water supply, distribution will be controlled by other factors such as light,

82 *Relation of Transpiration to Assimilation in Steppe Plants*

soil aeration, soil structure and composition, etc. Apart from this, even when the moisture factor is at its minimum, economical water loss may be not the decisive factor.

The plants may adapt their root system either by developing it very vigorously in comparison with the leaves or by making it penetrate into the deeper layers or increase their water supply by other means. Under such conditions they may evaporate less economically, and the figures may therefore lead to other results. Generally the plant can adapt itself to the hard conditions of life not only by regulating its aerial parts but also by adapting its subterranean organs. Another choice of plants would probably give no such striking results.

The experiments here described simply show that we may expect to find in drought-resistant plants a more economical evaporation of water.

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THE OAK-HORNBEAM WOODS OF HERTFORDSHIRE PARTS I AND II

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(With Plates IX and X and five Figures in the Text)

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PART I. GENERAL AND INTRODUCTORY

The subject-matter of the present paper is based chiefly upon detailed observations made during the past five years. In the course of the investigation most of the more important woods in Hertfordshire have been visited. Observations of a general character have extended over a much longer period. The author is glad of this opportunity of expressing his great indebtedness to the Rt Hon. the Marquis of Salisbury, Lieut.-Col. A. D. Acland,

Mrs Burns, Mr H. B. Cox, Mr Roger Cunliff, Mr G. Levinge Whately, and other owners and tenants for the free access to their woods which they have so generously afforded. The work has also been greatly facilitated by the readiness with which the agents of the estates visited and also the keepers have afforded information on various points.

(1) **Historical Evidence and Status of the Oak-Hornbeam Woods.**

The county of Hertford is in the main an agricultural district, as a consequence of which the area occupied by woodland is not large. The Board of Agriculture returns for 1905 show however that at that time 26,568 acres were occupied by woods of which 3724 acres represent areas afforested since 1881. By far the larger part of these woods are oak woods, dominated either by *Quercus robur* or *Quercus sessiliflora*, the former being associated with the heavier clays and clayey loams whilst the latter is mainly found on the lighter loams and sandy soils. In a large proportion of the oak woods the shrub-layer is extensive and periodically coppiced. It is quite clear from documentary evidence that the whole of Hertfordshire was at one time very densely wooded and that the present woods and copses are mere relics of the former forests. Thus in Domesday Book (ca. 1086) Hertfordshire, with its area of 611 sq. miles, is given as affording pannage for 30,720 swine, a large number, since Essex, with an area of 1657 sq. miles, and which was almost continuous forest, is given as only having woodland enough to feed 92,991 swine. In an early manuscript, entitled "The Characteristics of Counties," published in Hearne's edition of Leland's *Itinerary*, Hertfordshire is referred to as "ful of wode." We are here only concerned with a portion of the Hertfordshire woodlands, namely the oak-hornbeam woods, in which the undergrowth consists mainly of *Carpinus betulus*. This type of oak wood is here described in detail for the first time. The remarks which have been made above with respect to Herts. woodlands in general probably apply with equal force to the particular type we are considering. Thus we find that the areas which are now occupied by small and scattered oak-hornbeam copses formerly supported large numbers of swine (e.g. Wheathampstead 400 swine, Sandridge 300 swine). It is particularly in the south-east of the county that the hornbeam becomes most abundant, associated with the *Quercus sessiliflora* woods. This fact was pointed out by Coleman and Webb¹. "In the Lea division of the county, especially in the south, it (the hornbeam) forms the principal part of the underwood, hence we may name this district the Regio Carpinii." In the west the woods are mostly oak-hazel, whilst between these two types lie the *Q. robur-Carpinus* woods (Fig. 7).

Kalm², too, states that between Cheshunt and Bell Bar "in some places there were hornbeam-trees enough six feet high and tolerably thick. The

¹ "Flora Hertfordiensis," p. 270.

² "En Resa till Norra America...af Pehr Kalm," Stockholm, 1753-56 p. 184.

tops were cut for fuel, otherwise they were of no particular use." Again at Little Gaddesden, where the woods at the present time are mostly oak-hazel, he states "the hornbeam was here very rare¹."

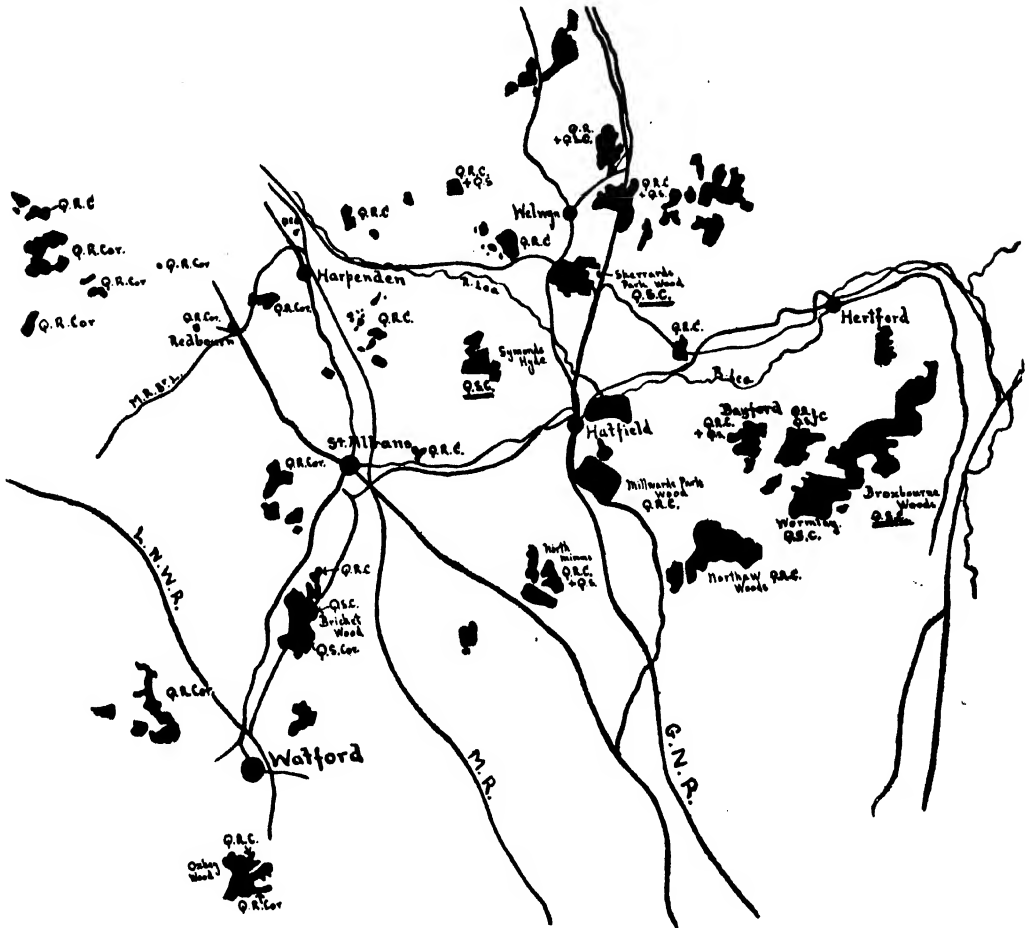


FIG. 7. Map of a portion of Hertfordshire showing the distribution of the different types of woodland. The *Quercus robur-Corylus* (*Q.R.Cor.*) woods are situated chiefly in the west and the *Q. sessiliflora-Carpinus* woods (*Q.S.C.*) to the south-east. Between the two lie the *Quercus robur-Carpinus* woods (*Q.R.C.*) dealt with in Part II.

The question naturally arises as to whether the hornbeam undergrowth is a natural product or the result of planting. That planting of hornbeam was practised is certain. Thus Ellis², who lived at Little Gaddesden, writes, "This (the hornbeam) is in great reputation for both copse-hedge and wood and is planted in many parts, but more abundantly about Whethamsted in this County." The natural character of this type of undergrowth is

¹ The author is indebted, for this translation from the Swedish original, to Dr B. Daydon Jackson.

² "The Timber Tree Improved," London, 1742, p. 71.

however supported by the following facts. (1) Association with definite types of soil. (2) The replacement of *Carpinus* by *Corylus* or *Sambucus* in different parts of the same wood, where there is a local change in the soil-conditions. (3) A ground-flora that differs in composition from that of the oak-hazel woods. (4) The occurrence of rare or local species, such as do not occur in woods known to be of recent origin. (5) The presence of a number of associated shrubs. (6) The occurrence of oak-hornbeam woods on similar soil in Essex, Kent and Middlesex.

These points will be dealt with in the sequel, but with regard to the first we may note that Schlich¹ states that "loams, sandy soils rich in humus, and marls suit it best." According to Correvo² "il recherche les sols argilosablonneux frais et permeables." Loudon³ also mentions that the hornbeam will not thrive on chalk. It is clear then that both in England and on the Continent the hornbeam naturally occurs on the lighter types of soil. On the other hand the hazel is commonly found on heavy types of soil and on soils rich in calcium carbonate.

The hornbeam woods of Hertfordshire are likewise associated with the lighter types of non-calcareous soil. Furthermore in these woods the hazel is often abundant, where the soil becomes heavy, and even occurs as a pure undergrowth, or associated with *Sambucus*, where the soil is calcareous or very wet.

The oak-hornbeam wood finds a place in the enumeration of British woodlands, given by Moss⁴, an inclusion that was adversely criticised by Tansley⁵ on the grounds that "there is no evidence that the presence of the hornbeam modifies the associated vegetation." Whether we are dealing however with the chief types of woodlands or their sub-types, the ground-flora is not merely dependent upon the character of the tree and shrub layer, but trees, shrubs and ground-flora, constituting the ecological assemblage, are *together* an expression of the *combined influences* of soil, climate, and situation, as well as the interaction of the plants themselves. If, therefore, it can be shown that the presence of a hornbeam shrub-layer is associated with other floristic differences, whether in kind or relative amount, and that these can moreover be correlated with different edaphic or climatic conditions or both, we shall be justified in regarding the oak-hornbeam wood as a definite sub-type, even if it were not true that the change in undergrowth itself probably affects the ground-flora.

¹ "Manual of Forestry," 2, p. 334.

² "Nos Arbres," Paris, 1906, p. 243.

³ "Encyclopedia of Trees and Shrubs," London, 1842, p. 918.

⁴ "Vegetation of the Peak District," Cambridge, 1913, p. 39.

⁵ This JOURNAL, 1, 1913, p. 278.

(2) Climatic Conditions¹.

The mean annual temperature of Hertfordshire deduced from records extending over a period of 25 years is 48.4° F. (9.1° C.). The monthly mean and the range during the same period is given in Table I. The means show

TABLE I. *Temperature*

Months	Mean	Average Max.	Average Min.
Jan.	37.3° F.	42.2° F.	32.4° F.
Feb.	38.2	43.8	32.5
March	41.1	48.2	34.0
April	46.1	54.6	37.4
May	51.0	61.0	42.8
June	57.9	67.0	48.7
July	61.3	70.5	52.1
Aug.	60.6	69.5	51.7
Sept.	56.5	65.0	48.0
Oct.	49.0	55.9	42.1
Nov.	42.8	48.5	37.2
Dec.	38.6	43.5	33.7
Year	48.4	55.8	41.0

that January is the coldest and July the warmest month, whilst between the two the mean temperature shows an upward gradient which becomes pronounced from March onwards. The mean annual rainfall for the 70 years 1840–1909 is 26.04 inches, the driest months being February, March and April. Table II gives the monthly means and the average number of days on which more than 0.01 inch of rain fell during the period 1870–1909.

TABLE II. *Rainfall and Humidity*

Months	Mean Rainfall, 1840–1909	No. of days, 1870–1909	Humidity (%), 1887–1911
Jan.	2.17	15	91
Feb.	1.66	14	88
March	1.71	14	84
April	1.69	13	76
May	2.01	13	73
June	2.14	12	73
July	2.46	13	71
Aug.	2.47	14	74
Sept.	2.22	12	80
Oct.	2.96	17	87
Nov.	2.46	16	91
Dec.	2.09	16	92
Year	26.04	169	82

In comparing the vegetation of the oak woods here described with the *Quercus robur* woods described by Moss², Wilson³ and Adamson⁴, it must be noted that the mean annual rainfall for Kent and Cambridgeshire is

¹ These data are compiled from the account by **Hopkinson** ("The Climate of Hertfordshire," *Trans. Herts. Nat. Hist. Soc.*, **15**, Part iv, 1915, pp. 195–206).

² "Geographical Distribution of Vegetation in Somerset," London, 1907.

³ "Plant-distribution in the Woods of North-east Kent," *Ann. of Bot.* **25**, 1911.

⁴ "An Ecological Study of a Cambridgeshire Woodland," *Journ. Linn. Soc.* **40**, 1912.

lower than that in Hertfordshire, whilst that of Somerset is higher. The mean annual temperature in all three counties is higher than that of Hertfordshire.

TABLE III. *Dates of Flowering of Plants*¹

Plant	Average for 20 years, 1891-1910						Aver. 37 years, 1876-1912 Hertfordshire
	Eng. S.W.	S.	Mid.	E.	N.W.	N.E.	
<i>Corylus avellana</i>	40	35	43	36	44	50	30
<i>Anemone nemorosa</i>	86	83	89	88	92	94	83
<i>Prunus spinosa</i>	92	98	100	99	104	109	95

Phenological observations (see Table III) show that Hertfordshire is slightly earlier than the south of England.

PART II. THE *QUERCUS ROBUR-CARPINUS* WOODS

(1) General.

The hornbeam shrub-layer appears to be typically associated with the *Quercus sessiliflora* woods of Hertfordshire, and the *Quercus robur-Carpinus* woods, with which the present part deals, are probably to be regarded as a type transitional to the *Quercus robur-Corylus* woods. These transitional woods are often of no great area, being in many cases not more than 6 to 20 acres in extent. The small size and scattered distribution of such copses is a further argument in favour of their being relics of larger woods. In many cases they probably owe their immunity from the general conversion of woods into arable land, to the fact that they are often situated where the contour of the surface shows abrupt changes. Owing to the difficulties of ploughing, etc., such would naturally be the last areas to pass into cultivation.

It is chiefly smaller woods of the *Quercus robur-Carpinus* type, varying in extent from 3 to 60 acres, which have been critically examined and in this way an aggregate of over 100 acres of woodland has been under continued observation at all seasons of the year. On these observations the frequencies are mainly based, and it may be emphasised that such data are only reliable when, as in the present case, the same areas are repeatedly visited throughout the vegetative period. In addition, however, a very much larger area (some 1200 acres) of this type comprising woods from one-fifth to over half a square mile in extent have been also examined in detail at less frequent intervals. The lists of species embody the records thus obtained and also such additional ones as are given in Pryor's *Flora of Hertfordshire* (London, 1887).

¹ Compiled from **Hopkinson**, "Phenological Observations in Herts. for 1913" (*Trans. Herts. Nat. Hist. Soc.* **15**, 1915, p. 243), and **Clark** and **Hooker**, "Report on Phenological Observations for 1911" (*Q. J. Roy. Met. Soc.* **28**, 1912).

(2) **Edaphic Conditions.**

The *Quercus robur-Carpinus* woods occur in all the cases examined on the lighter clays and stiff loams. Most commonly these belong to the deposit known as clay with flints which forms a layer of very variable thickness overlying the chalk. It is therefore of interest to note that Wilson¹ records the occurrence of *Quercus robur* woods on the clay with flints of Kent in which *Carpinus* and *Fraxinus* are the most abundant members of the undergrowth. Owing to the piped character of the underlying chalk not only are the changes in depth often very abrupt, but, as has been pointed out by Woodward², the soil in consequence probably dries more readily after heavy rainfall.

In general the chalk subsoil is seldom less than three feet below the surface. For the first 6 to 12 inches the clay is more or less flocculated, probably owing to the high acidity (*vide infra*). Below this depth it passes into a yellow and stiffer clay that at about 2½ feet becomes quite colloidal. The upper layers sometimes contain so large a proportion of flints, an inch or more in diameter, that it is often difficult to insert a trowel for a depth of more than a few inches. In a sample of soil from Stocking's Wood the stones over 3 mm. in diameter represented 34·5 per cent. of the dry weight. The mechanical composition of the soil is somewhat variable but shows much the same proportions of coarse and fine particles as the clay with flints of Kent.

TABLE IV. *Composition of Woodland Soils (Quercus robur-Carpinus)*

	Stocking's Wood	Langley Wood
Fine gravel (over 1 mm.)	7·8 %	6·5 %
Coarse sand (0·13-1 mm.)	3·5 %	6·9 %
Fine sand, silt and clay (under 0·13 mm.)	84·2 %	61·9 %

Comparison shows that the soil in *Quercus robur-Corylus* woods usually contains a smaller proportion of gravel and coarse sand, whilst that of the *Quercus sessiliflora* woods contains a much higher percentage.

Humus. The organic content of the soil shows considerable variation even in the same wood and this is accompanied by variation in the character of the ground-flora. In general the humus is seldom below 7·5 per cent. and rarely above 15 per cent. of the dry weight (cf. Table XI, p. 103).

Water-content. The natural water-content has been determined for a number of woods at different periods of the year. These were based on composite samples placed in tins immediately upon collection, the soil was then dried at 100° C. till a constant weight was obtained. The samples were taken to a depth of 6 inches after the raw humus and vegetation had been

¹ *Loc. cit.*

² "Summary of Progress of the Geological Survey of the United Kingdom," London, 1903.
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water-content was recorded during the drought of 1915 towards the end of which as little as 19 per cent. of water was present.

Acidity. The author is indebted to Dr H. B. Hutchinson for the determinations of soil-acidity. These are expressed as the amount of lime required to neutralise, and the method employed is that described by Hutchinson and MacLennan in their paper on the lime requirements of soils¹.

TABLE VI. *Soil-acidities (composite samples from Quercus robur-Carpinus woods)*

Wood	Condition	Character of vegetation	Acidity	Acidity Humus
Secret Spring	Uncoppiced	Open (Anemone)	0.5 %	1 : 17.4
" "	"	Deep shade	0.42	1 : 24.5
" "	"	Mercurialis	0.34	1 : 32.6
" "	"	Dense Mercurialis	0.32	1 : 52
" "	"	"	0.72	1 : 25.4
" "	"	Scilla, Galeobdolon, Mercurialis	0.38	1 : 24.7
Stocking's Wood	"	Scilla, Anemone, Mercurialis	0.44	
Secret Spring	Coppiced	Holcus, Anthoxanthum, Cnicus	0.52	1 : 20.9
" "	"	" "	0.48	1 : 19
" "	"	Agrostis alba, Scilla	0.58	1 : 19
" "	"	Mercurialis, Scilla	0.24	1 : 40
" "	"	Mercurialis, Ficaria	0.31	1 : 41
" "	"	Near edge (Holcus, Anemone)	0.62	1 : 14.5
Stocking's Wood	"	Composite from various types	0.46	
Well Wood	"	" "	0.54	1 : 15
Average	Uncoppiced	" "	0.44	1 : 29.4
"	Coppiced	—	0.47	1 : 24.2

Table VI shows that the soil-acidity is high, corresponding to or even in excess of the higher acidities of a Heath in the same region². Since the effect of acidity is dependent upon the concentration the ratio of acidity to organic material gives us a measure of the normal acidity of the soil-solution.

(3) Light Conditions.

For the purpose of this paper the light-intensities were estimated by means of an actinometer. The time of exposure required for the sensitised paper to reach a standard tint being, as shown by Bunsen and Roscoe, inversely proportional to the intensity of the photochemical rays. Exposures of orthochromatic plates with yellow screens based upon such light-estimations seem to justify the assumption that the effect of different degrees of shading does not materially alter the relative proportions of the light of different wave-lengths. We may therefore regard the light-values obtained by means of the actinometer as approximately proportional to the photosynthetic value of the light. As is well known, however, the light-intensity on a sunny day is in excess of that which the green leaf is capable of utilising³.

¹ "Studies on the Lime-requirements of certain soils," *Journ. Agric. Sci.* **7**, 1915, pp. 75-105.

² Hutchinson and MacLennan, *loc. cit.* p. 102.

³ Brown and Escombe, "On the Physiological Processes of Green Leaves," *Proc. Roy. Soc.* **76**, 1905, pp. 54-55.

Blackman and Matthaei¹ estimated that, to prevent photosynthetic waste in sunshine, an increase of the carbon dioxide content of the air six-fold would be necessary. Since, as numerous investigators have shown, the assimilatory activity increases proportionately to the light-intensity, a diminution of the light to one-sixth would result in illumination becoming the limiting factor. In all cases the intensity of the *diffuse* light outside the wood was first estimated, and this was repeated after testing the intensity of the diffuse light in the interior of the wood. The light-intensity is throughout expressed as a percentage of the diffuse light-intensity in the open. Since diffuse light is approximately one-third the intensity of direct sunlight, a doubling of the carbon dioxide content of the air would result in the diffuse light-intensity becoming the limiting factor. Ebermayer working on the air in beech and pine woods found that the atmosphere two metres above the soil contained during the summer twice the amount of carbon dioxide of the air outside, i.e. 0.08 per cent., whilst the air in the humus layer contained no less than 0.148 per cent. CO₂.² Fodor³ and Russell and Appleyard⁴ have shown that the soil-air has a minimum CO₂-content during the summer and winter, whilst it attains a maximum during the late spring and autumn. Having regard to the relatively low growth of the social species of the ground-flora and the shelter they produce, the air around them probably has a much higher CO₂-content than the air in the open. From the data given above it is probably safe to assume that the diffuse light-intensity in a woodland is always the limiting factor to the photosynthetic activity when it falls below 50 per cent. of the intensity in the open, and very probably even when the diffuse illumination is at a maximum.

Owing to the seasonal changes of the shrub-layer we can clearly distinguish two phases in the light-conditions, namely (a) the *light-phase* extending from the leaf-fall in autumn to leaf-expansion in spring, and (b) the *shade-phase* from about the middle of May to autumn. During the former the shading effect mainly depends upon the horizontal branch-canopy of the standards and the bare twigs of the shrubs. The former is however probably more efficient in reducing the intensity than the almost vertically directed branch-systems of the shrub-layer. The intensity during the shade-phase is mainly conditioned by the age of the coppiced shoots.

¹ "Experimental Researches in Vegetable Assimilation and Respiration. IV. A Quantitative Study of Carbon Dioxide Assimilation and Leaf-temperature in Natural Illumination," *Proc. Roy. Soc. B*, **76**, 1905, p. 455.

² "Mitteil. ueb. den Kohlensauregehalt der Waldluft und des Waldbodens im Vergl. zu einer nicht bewaldeten Flaeche," *Forsch. auf d. Gebiete d. Agric. Physik*, **1**, 1878, pp. 158-161.

³ "Hygienische Unters. ueb. Luft, Boden, u. Wasser," Braunschweig, 1881.

⁴ "The Atmosphere of the Soil, its Composition, and Causes of Variation," *Journ. Agric. Sci.* **7**, 1915.

TABLE VII. *Light-intensities (Quercus robur-Carpinus woods)*

Locality		Age of coppice (years)	Light-phase (%)	Shade-phase (%)
Stocking's Wood	...	7	50-60	0.9
"	"	11	37-48	0.16-0.76
"	" (break in canopy)	11	—	5.4
Langley Wood	... Abt.	13	40-46	0.44-0.74
Pudler's Wood	...	14	29.1	
Cutts Green	...	4	61	1.3
"	" (between stools)	4	—	5.5
Eight Acre Wood	...	5	46-60	
"	"	6	41-55.5	0.78
Dowdell's Wood	...	17	38.4	0.83-1.1
Sauncy Wood	...	10	42-50	0.33-1.2
Clapper's Wood	...	12	—	1.28
Secret Spring	...	6	46	
"	"	7	33-40	0.36
Bladder Wood	...	20	24	
Milward's Park.	No undergrowth, open canopy	—	60	
Walshingham Wood	...	10	33-54	0.77
"	" (path)	—	50-100	
Northaw Great Wood	No undergrowth, dense canopy	—	37-40	
Total range	...	—	61-24	5.5-0.16
Average	...	—	41-48.8	0.8-1.4

The average intensity during the light-phase (see Table VII) rapidly falls as the undergrowth increases in age, so that during the greater part of the uncoppiced period, which usually lasts for 10 to 14 years, the light-intensity is from 40 to 60 per cent., but, during the last few years before coppicing, the intensity during the light-phase decreases to an average of between 30 per cent. and 45 per cent. of the total diffuse light outside.

During the shade-phase the illumination is much less uniform, varying between 0.16 per cent. and 1.3 per cent. where the canopy is continuous, though it may attain to 5 per cent. where the canopies, formed by adjacent shrubs, meet. Along the paths the light-intensity may be as much as 20 per cent. or even more. For the typically woodland species, which are nearly all vernal, it is the illumination during the light-phase that is important. A study of the light-intensity at the same spot in a wood during the early part of the year (Fig. 8) shows a gradual increase during March, probably due to the increasing altitude of the sun. As the shrubs begin to enlarge during April the intensity decreases and then exhibits a rapid fall during leaf-expansion. In view of the very low intensity of light during the shade-phase of an uncoppiced wood it is evident that after the light-phase has ended assimilation can only be carried on very slowly by the leaves of the ground-vegetation. If we compare the light-intensity during the two phases we shall find that during the one it is nearly 35 times as great as during the other. Even plants then such as *Mercurialis perennis* and *Galeobdolon luteum* which, in the lighter parts of the wood may retain their leaves

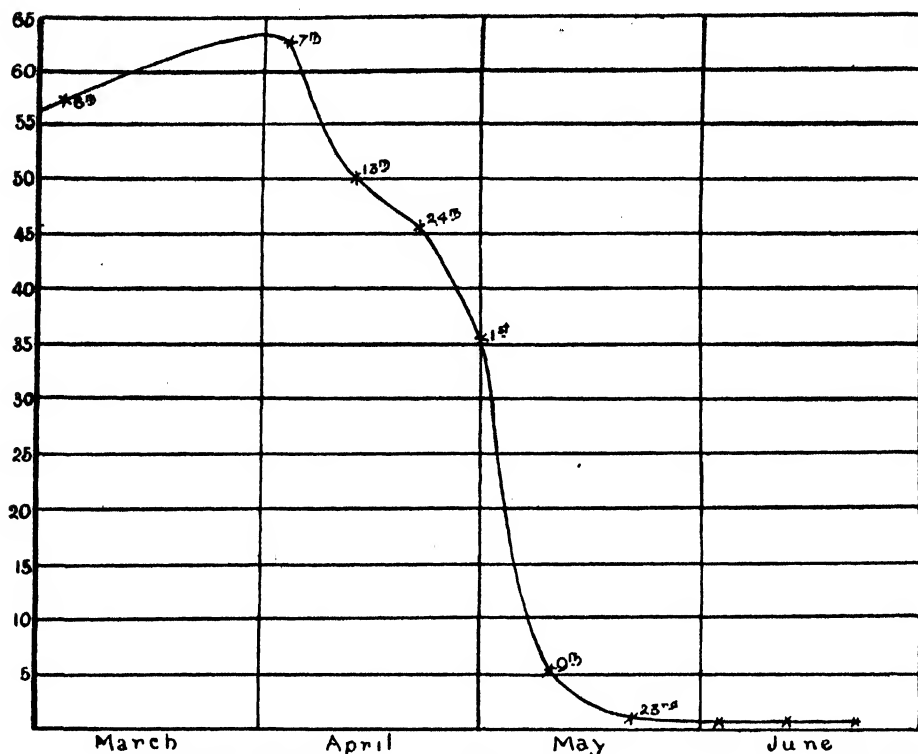


FIG. 8. Diagram showing changes in the light-intensity at one spot in a *Quercus robur*-*Carpinus* wood.

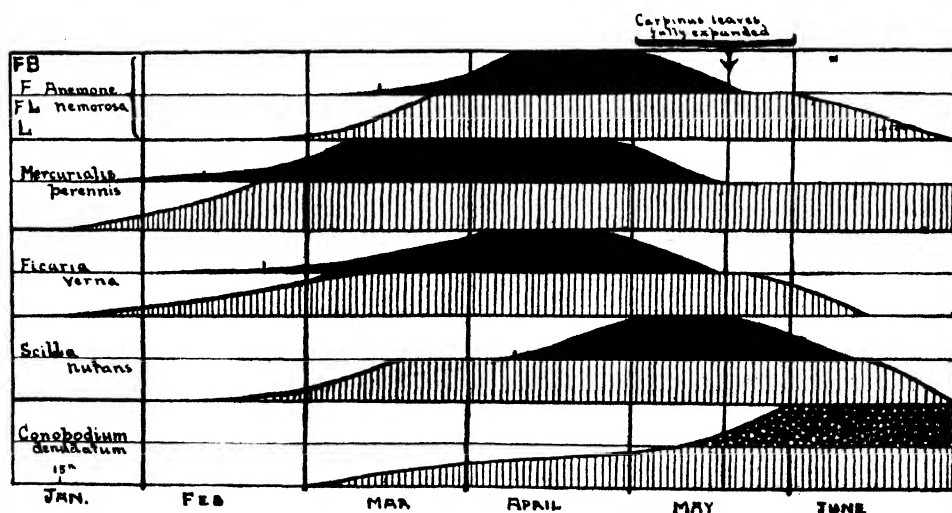


FIG. 9. Diagram showing the period of foliage and flower production for common species of the shade-flora based upon the average of several years. The vegetative period is shown by vertical shading and the flowering period black. F.L., full leaf; F.B., full bloom. The stippling indicates that flowering only occurs in the coppiced wood.

throughout the summer would, on the most generous computation, only receive during the entire shade-phase about one-fourteenth of the amount of light which reached them during the light-phase.

The period of foliage-formation for the different species is therefore of great importance in determining their capacity for vigorous growth in the interior of the wood. In Fig. 9 the vegetative periods for the more important shade-species are indicated as well as their periods of flower-production. In the case of *Ficaria verna*, *Mercurialis perennis* and *Primula acaulis* the new leaves may have already developed by the middle of January, those of *Scilla nutans* and *Arum maculatum* begin to appear about the middle of February, whilst *Galeobdolon luteum*, *Conopodium denudatum* and *Anemone nemorosa* do not usually produce their foliage till early in March. It is therefore significant that *Ficaria*, *Mercurialis* and *Primula* are met with in the deeper shade, whilst *Anemone*, *Conopodium* and *Galeobdolon* are more particularly associated with the better lighted areas. Since the early production of assimilating organs is so important a factor in the nourishment of woodland species it is interesting to note that in some of these plants the last season's leaves often in part persist through the winter. Examples are afforded by *Galeobdolon luteum*, *Primula acaulis*, *Sanicula europaea*, *Nepeta glechoma*, *Stellaria holostea* and *Viola riviniana*. An examination of a wood on January 9th, 13 months after coppicing, where the exposure consequently was still considerable, revealed a number of species with green leaves persisting from the previous season or, in most cases, the product of new growth. These included *Ajuga reptans*, *Ficaria verna*, *Fragaria vesca*, *Galeobdolon luteum*, *Geum urbanum*, *Holcus lanatus*, *Hypericum perforatum*, *Mercurialis perennis*, *Nepeta glechoma*, *Orchis mascula*, *Potentilla fragariastrum*, *Primula acaulis*, *Ranunculus auricomus*, *Rumex condyloides*, *Sanicula europaea*, *Stellaria graminea*, *Veronica chamaedrys* and *Viola sylvestris*. Besides these there were the woodland annuals, namely *Galium aparine*, *Arenaria trinerva* and *Torilis anthriscus*, which it is interesting to note germinate the previous autumn and retain their foliage throughout the winter.

An exception to the above generalisation appears to be afforded by *Epipactis violacea* which does not produce its leaves until after the inception of the shade-phase and often grows in situations where the canopy is moderately dense. Probably, however, the explanation lies in the fact that the nutrition of this plant is, like so many of the orchids, largely saprophytic.

The early flowering of woodland plants is doubtless related to the necessity of light for their proper development. A study of the flowering period of British woodland plants shows that in general they flower nearly a month earlier than non-woodland species (Fig. 10). As a consequence of this fact the advent of the shade-phase will only affect the production of flowers adversely towards the end of the flowering period. In *Oxalis acetosella* and *Viola* spp. the normal flowers are replaced during the shade-phase by

cleistogamic ones, but in most species flower-production ceases after leaf-expansion of the shrub-layer. That flowering is largely dependent upon the photosynthetic activity would appear to be indicated by the fact that shade frequenting species blossom most profusely in a coppiced wood (compare Phot. 8, Plate X, with Phot. 2, Plate IX), and they exhibit a diminishing flower-production as the coppiced shoots increase in size and the illumination during the light-phase decreases. As will be seen from Fig. 8 the light-intensity begins to diminish slightly some time before actual leaf-expansion, hence we

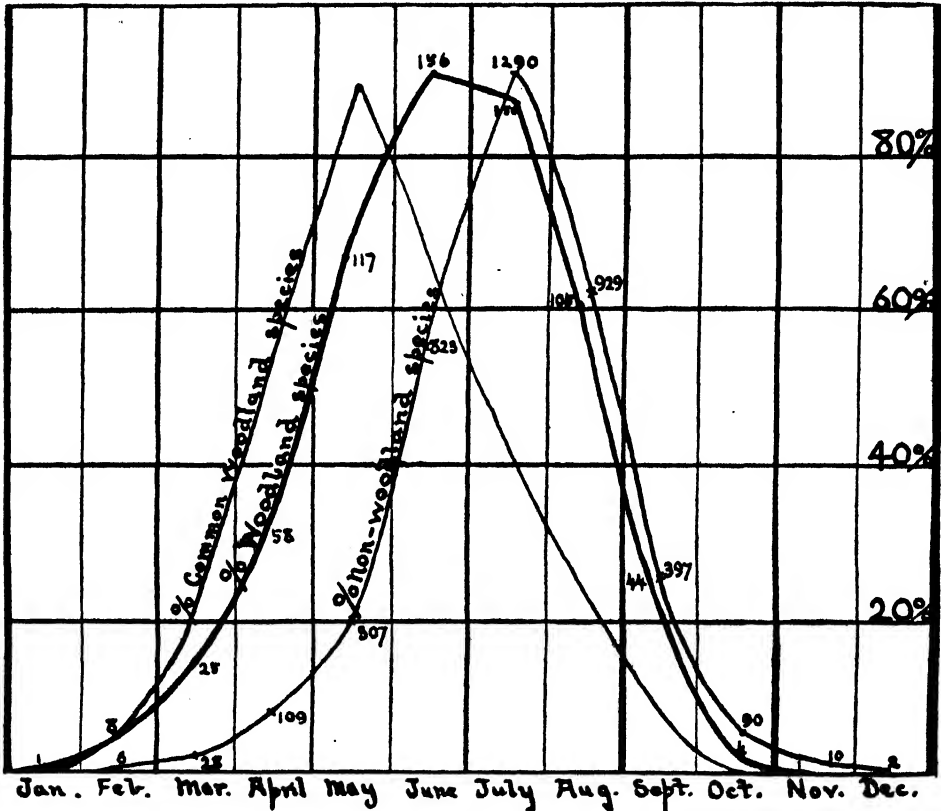


FIG. 10. Diagram showing the percentage of woodland and non-woodland species in the British Flora flowering in the different months.

can understand why it is that *Anemone*, *Galeobdolon* and *Conopodium*, which produce their foliage relatively late, are much more adversely affected than such species as *Ficaria verna* and *Mercurialis perennis*. Most woodland species have food-reserves formed in the previous season upon which the production of flowers depends. We can therefore understand why coppicing which usually takes place in January or February does not materially affect flower-production during the same season. In the next year however such plants as *Anemone*, *Conopodium*, and *Galeobdolon* often produce a wealth of bloom that is almost phenomenal (Plate X, Phot. 8).

The light-phase is then the critical period and the amount and vigour of the ground-flora would appear to be mainly dependent on the intensity of the light at this time. It is a well-known fact that the floor of a pine wood, a box wood or a beech wood is frequently devoid of vegetation except for a few bryophytes and fungi. Light-tests, in woods belonging to these types, reveal the fact that the light-intensity in such woods, during the shade-phase is often not less than in oak woods with a well-grown coppice, in the latter however there is often a considerable vernal ground-flora (see Table VIII).

TABLE VIII. *Light-intensities (woods without ground-flora)*

Wood		Light-phase	Shade-phase
Pine wood, Wisley	...	4.3 %	
Box wood, Boxhill	...	1.33 %	
Beech wood, Berkhamstead		—	0.4 %
„ Pitstone	...	19.4 %	1.4 %
„ Aldbury	...	40 %	1.6 %
„ „	...	38 %	1 %

The absence of ground-flora from such woods is therefore probably due, in the case of the pine and box, to the permanent character of the shade-phase. In the case of the beech, to the low intensity during the light-phase and to the fact that the ground-flora does not receive any periodic impetus through the coppicing of an undergrowth. In other words it is the intensity during the light-phase combined with the time-factor which determines the amount of the ground-flora, the intensity during the shade-phase being relatively unimportant. It is in complete accord with this view that even the vernal shade-flora of an oak wood tends to become more and more scanty the longer the coppiced stools remain uncut (Plate X, Phot. 6), and those species that persist do so in spite of the adverse conditions. The longer the latter prevail the more completely do the light-demanding species become eliminated, whilst those which can endure shade will only survive as scattered individuals, particularly near the margin of the wood. Thus in the case of Bladder Wood (Table VII), where the intensity during the light-phase is only 24 per cent. and the coppice-shoots 20 years old, the ground-flora is extremely sparse and large areas are completely bare. Dowdell's (17 years) and Pudler's (14 years) with average light-intensities of 38.4 per cent. and 29.1 per cent. respectively show the same phenomenon in a less marked degree. It is important to note that of these two woods that having the older coppice has the greater paucity of vegetation, although the average light-intensity is higher than that of the younger coppice. This clearly indicates that reduced illumination requires a period of years for the full effect to become manifest and consequently explains the occasional survival of light-demanding species in the interior of woods where the interval between successive coppicings is short.

In some woods where the tree layer is sufficiently dense to form an almost continuous canopy the shrub layer is very sparse or altogether absent. In such woods the light-intensity during the light-phase may be higher than in those woods with a sparse tree layer and dense shrub layer (e.g. Northaw, Table VII), and yet the ground-flora is usually extremely scanty, whilst that where the shrub layer is dense, unless it be old, is abundant. Here again the time-factor is probably all important, even the shade-enduring species becoming greatly reduced during the long interval between successive fellings. This aspect will be again considered in relation to the effect of coppicing, but we may summarise the results by saying that the ground-flora of the uncoppiced wood is to be regarded, in the main, as a relic from the periodically recurring intervals of increased illumination. Where these have been frequent (short coppice period) the ground-flora is abundant, where infrequent (long coppice period), or at long intervals (felling), the ground-flora is scanty.

(4) **The Flora of the Uncoppiced Wood.**

(a) *The Tree Layer.* The predominating tree in these woods is undoubtedly *Quercus robur*. The number of standards per acre is not usually large (about 60), and sometimes does not exceed an average of 5 per acre. On the lighter soils occupied by *Quercus robur*-*Carpinus* woods occasional specimens of *Quercus sessiliflora* are usually present. Some, if not all, of these woods in which both species occur are very probably to be regarded as of the *Quercus sessiliflora*-*Carpinus* type in which, owing to felling of the original species and the planting of *Quercus robur*, only a few self-sown relics of *Quercus sessiliflora* remain. In any case such woods constitute a transition, both as regards the arboreal and herbaceous flora, to the *Quercus sessiliflora*-*Carpinus* woods proper.

In some of the smaller copses trees of *Prunus avium* are often nearly as frequent as the oak itself, but this species appears to exhibit a decided preference for the heavier types of soil and is indeed a marked feature of the oak-hazel woods. The ash is also of very general occurrence, especially in the wetter parts or where the underlying chalk approaches close to the surface. In clearings the ash is often the dominant tree and dense thickets of ash saplings usually occupy disused rides, etc., which have been left uncleared for some time (Plate X, Phot. 5). *Ulmus montana* though never common is quite characteristic. On the lighter soils and in the mixed woods in which *Quercus sessiliflora* is present, *Betula alba* and *B. pubescens* are both frequent, the white birch being usually the commoner.

Of the smaller trees the most characteristic are *Salix cinerea* and *S. caprea*, whilst on the lighter soils *Carpinus betulus* occurs frequently in this form. *Pyrus aucuparia* and *P. torminalis* appear to be restricted to those woods in which *Quercus sessiliflora* is also present. For lists, see Table X.

(b) *The Shrub Layer.* The density of the shrub layer is in inverse ratio to the proximity of the standards and, in general, the latter tend to be most numerous on the lighter types of soil. The undergrowth usually consists almost entirely of *Carpinus betulus* var. *provincialis* in the form of coppice, but it is important to note that in several woods the hornbeam is, locally, completely replaced by hazel. Striking examples are afforded by Oxhey Woods and North Mimms Woods, in both of these the hazel undergrowth is confined to those areas where, owing to the contour of the surface and the stiff character of the soil, the water-content is high.

TABLE IX. *Natural Water-contents*

Wood	Date	Carpinus		Corylus	
		Water-content	Humus	Water-content	Humus
Oxhey ...	14. iv. 16	35.4-36.8 %	7.4 %	50 %	11.32 %
North Mimms	25. iii. 16	31.1-37.4 %	8.2 %	44.5 %	11.1 %

The same feature can also be observed on a small scale in many of the woods where dells have been formed through excavation for chalk. Here hazel almost invariably occupies the slopes, whilst the floor where the soil is shallowest, i.e. nearest the chalk, is frequently marked by a dense growth of *Sambucus*. Occasionally small copses are even met with in which elder is throughout the predominating member of the undergrowth, but usually this type is very local and confined to the base of slopes or to shallow depressions where, either owing to the proximity of the chalk or the high water-content, the acidity is relatively low. The occurrence of species, which normally occur on chalk, in damp situations has already been recorded. Thus Moss¹ writing of the Pennine Woods says, "it seems clear that in any given natural station the abundance of the ash is due to one of two causes, either to a high water-content or to a high lime-content." Amongst the common shrubs found in chalk-scrub we may note *Crataegus monogyna*, *Sambucus nigra*, *Acer campestre*, *Ligustrum vulgare*, *Solanum dulcamara* and *Rhamnus catharticus* as species which are also found quite characteristically in very wet situations. These facts seem to point to acidity as being the chief factor in determining their distribution. For the very dry habitat has at most a low acidity owing to the high lime-content, whilst the wet habitat has a low acidity owing to the dilution of the humic acids. Similarly in the ground-flora we find *Mercurialis perennis*, usually associated with calcareous soils, also frequenting the damper parts of these acid woodlands (cf. Table VI).

Brambles and honeysuckle are very characteristic but are not usually common except in the mixed woods where, as in the *Quercus sessiliflora* woods proper, they tend to become abundant. Where the chalk subsoil comes to the surface not only does hazel replace the hornbeam, but such

¹ "Vegetation of the Peak District," p. 69.

shrubs as maple, dogwood and blackthorn, as well as *Clematis vitalba*, become much commoner. *Prunus institia*, *Rosa micrantha*, and *Viburnum opulus* are confined to the mixed woods.

TABLE X. *List of Trees and Shrubs**Trees.*

<i>Quercus robur</i>	d.
„ <i>sessiliflora</i>	r-o (lightest soils only).
„ <i>robur</i> x <i>Q. sessiliflora</i>	o (mixed woods only).
<i>Acer pseudo-platanus</i>	r.
<i>Alnus glutinosa</i>	r (lighter soils).
<i>Betula alba</i>	vr-fc (lighter soils).
„ <i>pubescens</i>	f (absent from heaviest soils).
<i>Carpinus betulus</i> var. <i>provincialis</i>	r-f.
<i>Fagus sylvatica</i>	vr-f (light soils or chalk outcrops).
<i>Fraxinus excelsior</i>	o-f.
<i>Populus tremula</i> var. <i>sericea</i>	o-lf (lighter soils).
<i>Prunus avium</i>	f-c.
<i>Pyrus aucuparia</i>	r (mixed woods only).
„ <i>malus</i>	vr-rr (3).
„ <i>torminalis</i>	vr (mixed woods only) (2).
<i>Tilia europaea</i>	r-lf (? planted).
<i>Ulmus montana</i>	r-o.

Shrubs, etc.

<i>Carpinus betulus</i> , var. <i>provincialis</i>	vc-ab.
<i>Acer campestre</i>	r-f.
<i>Calluna vulgaris</i>	f (1).
<i>Clematis vitalba</i>	l.
<i>Cornus sanguinea</i>	r-f.
<i>Corylus avellana</i>	r-lc.
<i>Crataegus monogyna</i>	o-f.
„ <i>oxycanthoides</i>	o (lighter soils).
<i>Hedera helix</i>	o-la.
<i>Ilex aquifolium</i>	r (? planted on heavier soils).
<i>Lonicera periclymenum</i>	o-f.
<i>Prunus institia</i>	vr (mixed woods only).
„ <i>spinosa</i>	r-f.
<i>Rhododendron</i>	r-vc (lighter soils only, introduced).
<i>Rosa arvensis</i>	r-f.
„ <i>canina</i> , agg.	(edge only).
„ <i>micrantha</i>	(mixed woods only).
<i>Rubus fruticosus</i> , agg.	f.

(The following forms have been recorded: *R. affinis*, *R. leucostachys*, *R. lindleianus*, *R. radula*, and *R. rhamnifolius*.)

<i>Rubus idaeus</i>	vr-f (lighter soils).
<i>Ruscus aculeatus</i>	vr (1).
<i>Salix aurita</i>	l (3).
„ <i>caprea</i>	r-f.
„ <i>cinerea</i>	f.
<i>Sambucus nigra</i>	r-lf.
<i>Solanum dulcamara</i>	o-f (edge).
<i>Ulex europaeus</i>	(edge).
<i>Viburnum opulus</i>	r (mixed woods only).

The symbols employed are as follows: ab, abundant; vc, very common; fc, fairly common; c, common; f, frequent; o, occasional; rr, rather rare; r, rare; vr, very rare; l, local. A number in brackets following a frequency indicates the number of woods from which a species has been recorded when not of general occurrence.

(c) *The Ground-flora.* The character of the ground-flora is influenced very markedly by the nature of the upper layers of vegetation. Woods in which the standards are few, even where the shrub layer is dense, if regularly coppiced, generally exhibit an abundant spring-flora. On the other hand woods in which the standards are numerous, usually have a sparse herbaceous vegetation, except along the edges of the paths and rides and the margin of the wood. It has already been pointed out that this is probably mainly an effect of the diminished light (during the light-phase this may not be more than 37 per cent.) acting over a prolonged period, but it must be added that the light soils where a dense tree-layer usually obtains do not generally, under conditions of maximum illumination, bear so abundant a ground-flora as those of a heavier character. Occasionally however the two conditions of dense tree-layer and dense shrub-layer can be observed in different parts of the same wood, when the more abundant ground-flora in the latter case demonstrates the fact that light-intensity is the predominating factor.

We can recognise that the ground-vegetation is composed of several societies which appear to be chiefly related to differences in the degree of soil-moisture normally present. Each society is, under the appropriate edaphic conditions, quite distinctive, but just as there is every gradation from low to high water-content, so too there is every transition between the different societies, and consequently species that normally occur in the relation of dominant and subordinate may be present as co-dominants (Plate IX, Phot. 3).

Pteris Society. The driest society is that dominated by *Pteris* with which are usually associated *Scilla*, *Holcus mollis*, and *Anemone*, often however in very small amount. This society is but rarely encountered in the *Quercus robur-Carpinus* woods and then only on the lightest soils, usually occupied by the mixed woods of *Quercus robur* and *Q. sessiliflora*. Where the bracken covers any large area, there is often little undergrowth or the latter consists almost entirely of *Rubus fruticosus* (agg.) and *Lonicera periclymenum*.

Anemone Society. Next in order of increasing water-content is the *Anemone* society (Plate IX, Phot. 2), in which *Conopodium* and *Scilla* are often abundant species.

Mercurialis and Ficaria Societies. The damp parts of the wood are occupied by a society dominated either by *Mercurialis* or *Ficaria* (see Plate IX, Photos. 1 and 4). The two species are generally found in association, but their relative abundance varies greatly. *Scilla nutans* is often most abundant in the *Mercurialis* society.

The data given (Table XII) show that the water-content may be as high where *Mercurialis perennis* predominates as where *Ficaria verna* is the most abundant species, though in general the latter occupies the damper situations. The determining factor between the two appears to be light-intensity, the

more deeply shaded areas being occupied by *Ficaria*, with which *Arum maculatum* is frequently associated. We have already noticed that *Ficaria verna* produces its foliage earlier than almost any other woodland species. The large part of the light-phase which is thus available for its assimilation probably renders the plant better able to withstand extreme shade-conditions. Estimations of water-content after spells of dry weather show that the difference in water-content between the different societies is under these conditions much less. Thus in Dowdell's Wood the water-content in the *Anemone* society was 29.2 per cent., whilst that of the *Mercurialis* society, on the same day, ranged from 30 to 32.8 per cent. It is in fact only after heavy rainfall that the soil of the damper societies receives the maximum amount of water it is capable of retaining. In connection with the occurrence of *Mercurialis perennis* and *Ficaria verna* in situations of high water-content it is interesting to note that *Ficaria verna* possesses well-developed hydathodes

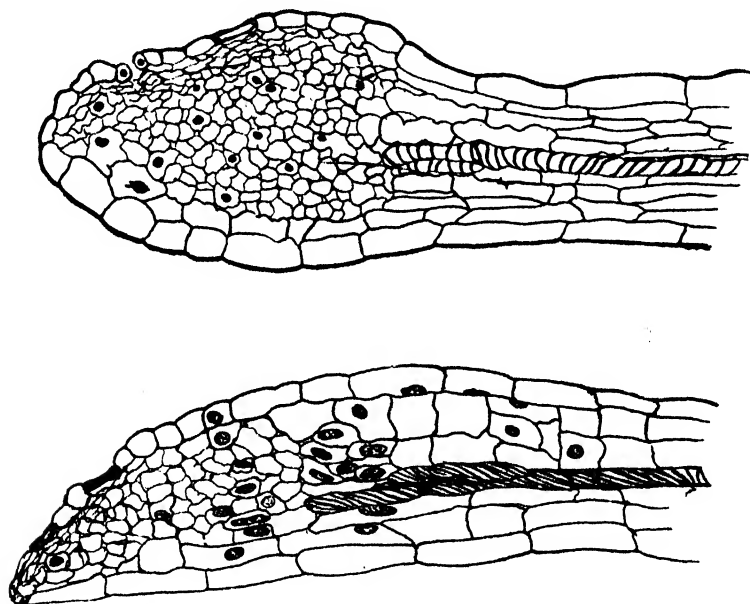


FIG. 11. Sections cut vertically through the leaf teeth of *Ficaria verna* (upper figure) and *Adoxa moschatellina* (lower figure) showing the hydathode in each case.

(Fig. 11), upon the margin of its leaves, which have been observed to actively secrete water under suitable conditions. The extrafloral nectaries of *Mercurialis* may also perform the same function. *Ranunculus auricomus* and *Adoxa moschatellina* (Fig. 11) which likewise possess efficient hydathodes are also particularly characteristic of the damper situations. From the estimations given (Tables XI and XII) it will be seen that the *Mercurialis* and *Ficaria* societies occupy the soil richest in humus, but the high water-content is often largely due to their frequently occupying situations at the base of slopes from which the drainage-water collects.

The *Mercurialis* society also occurs in these woods on shallow soil where the water-content is low but where the acidity is low also, on account of the close proximity of the chalk. This type of *Mercurialis* society is often found associated with an undergrowth of *Sambucus nigra* or *Corylus avellana*. The acidity determinations in Table VI show that the acidity where *Ficaria* and *Mercurialis* predominate is low, whilst where *Anemone* predominates the acidity is high.

Permanently moist depressions are almost invariably occupied by a *Ficaria* society (Plate IX, Phot. 4) accompanied or not by *Mercurialis* according to the light-intensity. In the wettest parts, subject to complete inundation in the winter-months *Ficaria* is accompanied or completely replaced by *Ranunculus repens*. The damp areas under trees forming a dense canopy and where there is no undergrowth are usually occupied by *Mercurialis perennis* (Plate IX, Phot. 1) and this species quite commonly forms patches beneath the canopy of isolated trees.

TABLE XI. *Organic Content of Soil in different Societies of the Ground-flora*

Wood	Character of vegetation	Organic content (%)
Hawkshead	Pteris dom	7.2
Oxhey	"	9.08
Milward's	"	5.36
Hawkshead	Anemone dom	8.2
Oxhey	"	7.4
Secret Spring	"	8.7
Well Wood (coppiced)...	"	8.1
Dowdell's	"	8.36
Stocking's	"	7.48
Cutts Green	"	9.4
Eight Acre	"	10.7
Secret Spring	Anemone-Scilla-Merc.	11.3
Marshall's	" " "	10.8
Langley Wood	" " -Ficaria	11.0
Secret Spring	Ficaria dom.	15.44
Well Wood (coppiced)...	"	11.4
Stocking's	"	15.52
Clapper's... ..	"	13.1
Secret Spring	Mercurialis vc	11.1
" "	" ab	16.8
" "	" ab	18.3
" "	" f	9.4
Hawkshead	Mercurialis-Ficaria	11.1
Oxhey	Mercurialis dom.	5.68
Mardley Heath... ..	"	6.08
Dowdell's	"	7.2
Pryor's	"	8.48
Milward's	"	11.44
Stocking's	"	18.72

Av. 7.21 %
Range, 5.36-9.08 %

Av. 8.5%
Range, 7.4-10.7 %

Av. mixed, 11 %

Av. 13.8 %
Range, 11.4-15.2 %

Av. 11.2 %
Range, 5.68-18.72 %

It may be noted that this situation is paralleled by the conditions in the average beech wood, where likewise there is a closed canopy and absence of undergrowth. In such a habitat the light-intensity during the shade-phase is higher than where there is undergrowth, and the fact that *Mercurialis* and *Pteris* both retain their foliage during the shade-phase may explain their preference for this type of situation.

Light-intensities during Shade-phase

Wood	Society	May	August
Langley	Anemone	0.74 %	0.44 %
Langley	Mercurialis	1.17 %	0.76 %

The occurrence of *Mercurialis* in such abundance in these acid woods can be reconciled with its prevalence on dry calcareous soils if we regard acidity as the chief factor regulating its frequency. The acidity of the *Mercurialis* society, if relatively high, is counterbalanced by the high organic content which involves a high water-content. Where the *Mercurialis* society is associated with a low water-content, the acidity is low also. Thus the habitats probably agree in possessing, even in the dry season, a low concentration of the acids present.

TABLE XII. *Water-contents of Societies*

Wood	Date	Society	Water-content (%)
Sauncy	13. ii. 16	Anemone	30.0
"	"	Ficaria	35.9
Langley	19. v. 15	Anemone	26.2
"	"	Mercurialis	33.3
Hawkshead	25. iii. 16	Pteris-Anemone	31.1
"	"	Anemone-Scilla	37.4
"	"	Mercurialis	44.5
Milward's Park	6. iv. 16	Pteris	36.2
"	"	Mercurialis	55.6
Stocking's "	3. i. 16	Anemone	32.5
"	"	Mercurialis	56.3
"	"	Ficaria	41.5
Dowdell's	10. iv. 16	Anemone	29.2
"	"	Mercurialis	30.0

Rarely in the mixed oak woods the *Ficaria* of the *Mercurialis-Ficaria* society is replaced by *Adoxa moschatellina*, and it is interesting to note that in all the observed cases the associated undergrowth consisted of *Corylus* occupying relatively shallow soil resting on the chalk. These facts harmonise with the occurrence of this society in the oak-hazel woods of the county and its prevalence in the ash woods of Somerset¹.

The shade-flora of the uncoppiced wood consists of few species, of which the most characteristic are *Anemone nemorosa*, *Mercurialis perennis*, *Scilla nutans*, *Ficaria verna*, *Conopodium denudatum*, *Arum maculatum*, *Primula acaulis*, and *Galeobdolon luteum*. In medium shade, not only are most of these species more vigorous, but in addition *Ajuga reptans*, *Viola sylvestris*, *V. riviniana*, and *Veronica montana* often become frequent. The remaining members of the shade-flora are either rare or confined to a few only of the woods. In the following lists the frequency symbols are intended as applying to the woods generally. Where a species is restricted to a few woods, the number in which it has been recorded is given in brackets.

¹ See Moss, in Tansley's "Types of British Vegetation," 1911, p. 151.

TABLE XIII. *List of Species in the Ground-flora**Deep-shade flora.*

<i>Adoxa moschatellina</i>	lf (2).
<i>Ajuga reptans</i>	o (medium shade—f).
<i>Anemone nemorosa</i>	vc-ab.
" " var. <i>robusta</i>	vr (1).
" " var. <i>apetala</i>	o.
<i>Arctium nemorosus</i>	r (medium shade—r-f).
<i>Arenaria trinerva</i>	vr.
<i>Arum maculatum</i>	f-c.
<i>Carex sylvatica</i>	vr.
<i>Conopodium denudatum</i>	f-vc.
<i>Epipactis latifolia</i>	vr (1).
" <i>violacea</i>	rr (2).
<i>Ficaria verna</i>	c-ab.
" " <i>forma incumbens</i>	vr (1).
<i>Galeobdolon luteum</i>	f.
<i>Geum urbanum</i>	vn.
<i>Helleborus viridis</i>	o-lf (4).
<i>Heracleum sphondylium</i>	vr-r.
<i>Iris foetidissima</i>	r-vr (chalk outcrops).
<i>Mercurialis perennis</i>	ab-vc.
<i>Narcissus pseudo-narcissus</i>	f-vc (3).
<i>Neottia nidus-avis</i>	vr (3).
<i>Orchis mascula</i>	lr-lf.
<i>Primula acaulis</i>	f.
<i>Ranunculus auricomus</i>	r-fc (damper woods).
" <i>repens</i>	rr-lc (very damp places).
<i>Sanicula europaea</i>	r.
<i>Scilla nutans</i>	a.
" " <i>forma alba</i>	r-vr (5).
<i>Viola riviniana</i>	vr (f in medium shade).
" <i>sylvestris</i>	r-vr (f in medium shade).
" " var. <i>punctata</i>	r-vr (f in medium shade).
<i>Aspidium filix-mas</i>	r-vr.
<i>Athyrium filix-foemina</i>	vr.
<i>Pteris aquilina</i>	r (ab in 2).

N.B. Of the above species, usually not more than about 12 are found in any one wood in the deep shade.

Additional species occurring in medium shade.

<i>Bryonia dioica</i>	r.
<i>Galium aparine</i>	r.
<i>Luzula pilosa</i>	r.
<i>Nepeta glechoma</i>	rr.
<i>Rumex condylodes</i>	rr.
<i>Scrophularia nodosa</i>	r.
<i>Sedum telephium</i>	vr (2).
<i>Urtica dioica</i>	r.
<i>Veronica chamaedrys</i>	r.
" <i>montana</i>	r-f.
" <i>officinalis</i>	r.

The following species have only been encountered in the ground-flora of woods where *Quercus robur* is accompanied by occasional trees of *Q. sessili-flora*, and, except where otherwise indicated, are of infrequent occurrence.

<i>Angelica sylvestris</i>	l (damper parts).
<i>Aquilegia vulgaris</i>	? extinct.
<i>Callitriche stagnalis</i>	fc (rides, etc.).
<i>Campanula latifolia</i>	lf (1).
" <i>trachelium</i>	lf (1).
<i>Carex divulsa</i>	

TABLE XIII (*continued*)

<i>Carex leporina</i> .				
" <i>muricata</i> .				
" <i>pallescens</i> .				
" <i>pendula</i>	f.
" <i>strigosa</i> .				
" <i>vesicaria</i> .				
<i>Dipsacus pilosus</i> .				
<i>Hypericum androsaemum</i>		r.
" <i>quadratum</i>		(rides, etc.).
<i>Lathyrus macrorrhizus</i> .				
<i>Limosella aquatica</i>		(rides, l).
<i>Luzula multiflora</i>		lf (coppice).
<i>Lychnis flos-euculi</i>		(damper spots).
<i>Mentha arvensis</i> .				
<i>Paris quadrifolia</i> .				
<i>Pedicularis sylvatica</i> .				
<i>Potentilla erecta</i> .				
" <i>procumbens</i> .				
<i>Scabiosa succisa</i> .				
<i>Scutellaria galericulata</i>		(rides).
<i>Stellaria uliginosa</i>		f (rides).
<i>Typha latifolia</i>		(ponds).
<i>Valeriana dioica</i> .				
<i>Aspidium dilatatum</i> .				
<i>Blechnum spicant</i> .				
<i>Equisetum sylvaticum</i> .				

(d) *Marginal and Path-floras*. By far the greater part of the ground-vegetation is to be found occupying the margin of the wood and the edges of the rides and paths. During the light-phase the intensity in these situations is seldom below 50 per cent. of the diffuse light outside and, even during the shade-phase, seldom falls below 5 per cent. whilst it is often over 20 per cent. As a consequence many plants which are relatively late in forming their vegetative organs and also flower late are able to occupy these situations. A complete list of the marginal and path-flora is given in Table XIV. Amongst the more characteristic members of the marginal society may be mentioned *Agrostis alba*, *Ajuga reptans*, *Anthriscus sylvestris*, *Arenaria trinerva*, *Brachypodium sylvaticum*, *Bryonia dioica*, *Calamintha clinopodium*, *Chaerophyllum temulum*, *Galeobdolon luteum*, *Galium aparine*, *Geranium robertianum*, *Heracleum sphondylium*, *Holcus lanatus*, *Melica uniflora*, *Nepeta glechoma*, *Poa nemoralis*, *Potentilla fragariastrum*, *Rumex condylodes*, *Sanicula europaea*, *Sisymbrium alliaria*, *Stachys sylvestris*, *Stellaria graminea*, *S. holostea*, *Tamus communis*, *Torilis anthriscus*, *Veronica chamaedrys* and *Vicia sepium*. Certain species appear to be confined to the actual paths themselves, possibly because these are often the dampest parts of the woods. None of these species is common, but *Gnaphalium uliginosum*, *Lysimachia nemorum*, *Poa annua*, *Prunella vulgaris*, *Ranunculus repens* and *Veronica montana* are especially characteristic of this situation.

The marginal flora has much in common with the flora of a hedgerow. Probably this is to be explained as due to the destruction of the primaeval forest which drove the species from the primitive scrub to seek sanctuary,

more and more, along the margins of the surviving remnants of woodland and in the artificially constructed hedgerows. The more open parts bearing scrub would naturally be the first areas to pass into cultivation. It is therefore highly probable that the proportion of scrub to woodland at the present day is very much lower than it was in primitive times.

TABLE XIV. *Path and Marginal Species and Coppiced Flora*

Species	Margin of woods and rides			Path	Coppiced areas
<i>Achusa cynapium</i> ...	—	—	vr (1).
<i>Agri-nonia eupatorium</i> ...	r	—	r.
<i>Agrostis alba</i> ...	f	—	f-vc.
„ <i>vulgaris</i> ...	—	—	r.
<i>Aira caespitosa</i> ...	r-f	r-f	—
„ <i>caryophyllea</i> ...	r	—	—
<i>Ajuga reptans</i> ...	f	f	f-c.
<i>Alchemilla arvensis</i> ...	—	c (1)	r (1).
„ <i>pratensis</i> ...	r (1)	—	—
<i>Anagallis arvensis</i> ...	—	r	r.
<i>Anthoxanthum odoratum</i> ...	—	—	f-vc.
<i>Anthriscus sylvestris</i> ...	f	—	f.
<i>Arctium nemorosus</i> ...	o-f	—	o-f.
<i>Arenaria leptoclados</i> ...	—	—	r (1).
„ <i>trinerva</i> ...	f	—	c-vc.
<i>Arrenatherum avonacum</i> ...	o	—	o.
<i>Asperula odorata</i> ...	rr-f	—	—
<i>Atriplex patula</i> ...	—	—	r.
<i>Barbarea vulgaris</i> ...	r	—	la.
<i>Brachypodium sylvaticum</i> ...	f	—	—
<i>Brassica sinapastrum</i> ...	—	—	vr (1).
<i>Bromus asper</i> ...	rr	—	—
<i>Bryonia dioica</i> ...	f	—	—
<i>Calamintha clinopodium</i> ...	f	—	r.
<i>Capsella bursa pastoris</i> ...	—	—	r (1).
<i>Cardamine flexuosa</i> ...	r (1)	—	—
<i>Carduus crispus</i> ...	o (3)	—	o (3).
<i>Carex binervis</i> ...	r (1)	r (1)	—
„ <i>sylvatica</i> ...	f-vr	—	o-f.
<i>Centaurea pratensis</i> ...	o	—	—
<i>Cerastium vulgatum</i> ...	r	—	o-r.
<i>Chaerophyllum temulum</i> ...	f	—	o-f.
<i>Chenopodium album</i> ...	—	—	vr.
„ <i>polyspermum</i> ...	—	—	f (1).
<i>Chrysanthemum leucanthemum</i> ...	—	—	vr (1).
<i>Circaea lutetiana</i> ...	r	—	—
<i>Cnicus arvensis</i> ...	r (2)	—	vr.
„ <i>lanceolatus</i> ...	o-f	—	r-f.
„ <i>palustris</i> ...	o	—	c-vc.
<i>Crepis virens</i> ...	—	—	r (2).
<i>Dactylis glomerata</i> ...	r	—	—
<i>Digitalis purpurea</i> ...	f (1)	—	—
<i>Dipsacus sylvestris</i> ...	r	—	rr-lc.
<i>Epilobium angustifolium</i> ...	r	—	r-o.
„ <i>montanum</i> ...	o-f	o	o-f.
„ <i>tetragonum</i> ...	o	r	—
<i>Erythraea centaureum</i> ...	—	—	f-c (lighter soils).
<i>Euphorbia amygdaloides</i> ...	o	—	o.
„ <i>exigua</i> ...	—	—	r.
<i>Fragaria vesca</i> ...	f-r	—	f.
<i>Fumaria officinalis</i> ...	—	—	r (1).
<i>Galeobdolon luteum</i> ...	f	—	c-vc.
<i>Galeopsis ladanum</i> ...	—	—	fc (1).
„ <i>tetrahit</i> ...	o	—	c-vc.

TABLE XIV (*continued*)

Species	Margin of woods and rides	Path	Coppiced areas
<i>Galium aparino</i> ...	f ...	— ...	f-c.
„ <i>mollugo</i> ...	o ...	— ...	r.
„ <i>palustre</i> ...	— ...	o (1) ...	—
„ <i>saxatile</i> ...	— ...	f (1) (light soils) ...	—
<i>Geranium columbinum</i> ...	— ...	— ...	o (2).
„ <i>dissectum</i> ...	o ...	— ...	f-c.
„ <i>molle</i> ...	— ...	— ...	r (1).
„ <i>robertianum</i> ...	o-f ...	— ...	r.
<i>Geum urbanum</i> ...	r-f ...	— ...	r-f.
<i>Gnaphalium sylvaticum</i> ...	— ...	— ...	f (1) (light soil).
„ <i>uliginosum</i> ...	— ...	r-rr ...	—
<i>Heracleum sphondylium</i> ...	f-c ...	— ...	f-c.
<i>Hieraceum boreale</i> ...	o (light soil) ...	— ...	—
„ <i>vulgatum</i> ...	o „ ...	— ...	—
<i>Holcus lanatus</i> ...	f ...	— ...	c-ab.
„ <i>mollis</i> ...	o (light soil) ...	— ...	r-vc.
<i>Hypericum humifusum</i> ...	— ...	vr ...	r.
„ <i>porforatum</i> ...	f-r ...	— ...	f-r.
„ <i>pulchrum</i> ...	r-vr (light soil) ...	— ...	r.
<i>Hypochaeris radicata</i> ...	— ...	— ...	r-lc.
<i>Juncus effusus</i> ...	lr ...	— ...	—
„ <i>supinus</i> ...	vr ...	— ...	—
<i>Lactuca muralis</i> ...	r (2) ...	— ...	—
<i>Lapsana communis</i> ...	r ...	— ...	r.
<i>Lathyrus nissolia</i> ...	r (2) ...	— ...	—
„ <i>pratensis</i> ...	o ...	— ...	—
<i>Listera ovata</i> ...	— ...	— ...	o.
<i>Lolium perenne</i> ...	— ...	— ...	vr (1).
<i>Luzula multiflora</i> ...	— ...	— ...	l (lighter soils).
„ <i>pilosa</i> ...	f ...	— ...	o-f.
<i>Lychnis dioica</i> ...	r (heavy soils) ...	— ...	r-f.
„ <i>vespertina</i> ...	r ...	— ...	r.
<i>Lysimachia nemorum</i> ...	r ...	r ...	r-f.
<i>Malva moschata</i> ...	vr ...	— ...	vr.
„ <i>sylvestris</i> ...	vr ...	— ...	vr.
<i>Matricaria inodora</i> ...	— ...	— ...	r (1).
<i>Melampyrum pratense</i> ...	r ...	— ...	f-vc.
<i>Melica uniflora</i> ...	c-f ...	— ...	—
<i>Melilotus officinalis</i> ...	— ...	— ...	f (2).
<i>Milium effusum</i> ...	o ...	— ...	—
<i>Myosotis arvensis</i> ...	rr ...	— ...	rr-c.
<i>Nepeta glechoma</i> ...	f ...	— ...	f-c.
<i>Orchis maculata</i> ...	r ...	— ...	o-fc.
<i>Oxalis acetosella</i> ...	f (light soils) ...	— ...	c.
<i>Papaver rhoeas</i> ...	— ...	— ...	vr (1).
<i>Peplis portula</i> ...	— ...	o (1) ...	—
<i>Picris echioides</i> ...	r (3) ...	— ...	lr (3).
<i>Pimpinella major</i> ...	r (3) ...	— ...	r (3).
<i>Plantago lanceolata</i> ...	— ...	— ...	f (1).
„ <i>major</i> ...	— ...	o ...	—
<i>Poa annua</i> ...	— ...	f ...	r-f.
„ <i>nemoralis</i> ...	f-c ...	— ...	f-c.
„ <i>trivialis</i> ...	o ...	— ...	o.
<i>Polygonum aviculare</i> ...	— ...	— ...	r-f.
„ <i>convolvulus</i> ...	— ...	— ...	o-f (4).
„ <i>lappathifolium</i> ...	— ...	— ...	f-c (2).
„ <i>persicaria</i> ...	— ...	— ...	o-f (2)
<i>Potentilla fragariastrum</i> ...	f ...	— ...	c-r.
„ <i>reptans</i> ...	— ...	o (2) ...	—
<i>Prunella vulgaris</i> ...	— ...	rr-f ...	rr.
<i>Ranunculus repens</i> ...	— ...	o-f ...	r.
<i>Rumex acetosa</i> ...	— ...	— ...	r (1).
„ <i>acetosella</i> ...	— ...	— ...	r-f (3) (light soils).

TABLE XIV (continued)

Species	Margin of woods and rides	Path	Coppiced areas
<i>Rumex condyloides</i> ...	f ...	— ...	f-lc.
„ <i>crispus</i> ...	r ...	— ...	r.
„ <i>obtusifolius</i> ...	o ...	— ...	lf.
<i>Sagina procumbens</i> ...	— ...	r (2) ...	—
<i>Sanicula europaea</i> ...	f-vc ...	— ...	f-vc.
<i>Scleranthus annuus</i> ...	— ...	r (2) ...	r (2).
<i>Scrophularia nodosa</i> ...	o-f ...	— ...	o-f.
<i>Senecio jacobaea</i> ...	— ...	— ...	r (1).
„ <i>sylvaticus</i> ...	r ...	— ...	r.
„ <i>vulgaris</i> ...	— ...	— ...	r.
<i>Sherardia arvensis</i> ...	— ...	— ...	r (1).
<i>Silene inflata</i> ...	r-f ...	— ...	r-f.
<i>Sisymbrium alliaria</i> ...	f-c ...	— ...	f.
„ <i>thalianum</i> ...	— ...	— ...	r (1).
<i>Solanum nigrum</i> ...	— ...	— ...	f (1).
<i>Solidago virgaurea</i> ...	r (2) (lighter soils) ...	— ...	r (2).
<i>Sonchus asper</i> ...	— ...	— ...	r-f (4).
„ <i>oleraceus</i> ...	— ...	— ...	vr (3).
<i>Spergula arvensis</i> ...	— ...	— ...	vc (1).
<i>Stachys betonica</i> ...	r (2) ...	— ...	—
„ <i>sylvatica</i> ...	f ...	— ...	f-c.
<i>Stellaria graminea</i> ...	f ...	— ...	f-c.
„ <i>holostea</i> ...	f ...	— ...	f-vc.
„ <i>media</i> ...	— ...	— ...	r.
<i>Tamus communis</i> ...	f ...	— ...	r.
<i>Taraxacum officinalis</i> ...	— ...	— ...	r (3).
<i>Teucrium scorodonia</i> ...	f (lighter soils) ...	— ...	f-c.
<i>Torilis anthriscus</i> ...	f ...	— ...	f.
<i>Trifolium repens</i> ...	— ...	r ...	—
<i>Triticum caninum</i> ...	o (2) ...	— ...	—
„ <i>repens</i> ...	r ...	— ...	—
<i>Urtica dioica</i> ...	r ...	— ...	r-f.
<i>Verbascum thapsus</i> ...	r ...	— ...	lf-rr.
<i>Veronica agrestis</i> ...	— ...	— ...	r.
„ <i>arvensis</i> ...	— ...	— ...	r.
„ <i>buxbaumii</i> ...	— ...	— ...	r.
„ <i>chamaedrys</i> ...	c ...	— ...	f-c.
„ <i>montana</i> ...	— ...	r f ...	r-c.
„ <i>officinalis</i> ...	— ...	r ...	r.
„ <i>serpyllifolia</i> ...	— ...	r ...	r.
<i>Vicia angustifolia</i> ...	r ...	— ...	r.
„ <i>hirsuta</i> ...	r ...	— ...	r.
„ <i>sativa</i> ...	— ...	— ...	rr (1).
„ <i>sepium</i> ...	f ...	— ...	rr.
<i>Viola arvensis</i> ...	— ...	— ...	r-rr.
„ <i>riviniana</i> ...	r-f ...	— ...	c-vc.
„ <i>sylvestris</i> var. <i>punctata</i> ...	f ...	— ...	c.

The following species occur in these woods, but are rare and restricted to local outcrops of chalk: *Carex glauca*, *Cephalanthera pallens*, *Daphne laureola*, *Habenaria chlorantha*, *Ophrys muscifera*, and *Viola hirta*.

(e) *Competition*. Competition between the species growing together may be the result of a struggle between the root-systems, between the aerial organs, or both. Species can only grow together without competition where their demands upon the soil are different or their roots are situated at different depths and their aerial organs are produced at different times of the year.

A study of the data given (Tables XV and XVI) shows that *Adoxa moschatellina*, *Anemone nemorosa* and *Ficaria verna*, all have roots situated at about the same level in the soil, and there is similarly competition between their aerial organs. We have already seen that these are species which tend to replace one another rather than to grow together. *Adoxa* and *Ficaria* are frequently found in association with *Mercurialis* and this is in harmony with the fact that the root-systems of the two former are at a different level from those of the last; both can moreover endure considerable shade. *Anemone* and *Conopodium*, which frequently occur together, produce most of their roots at different levels and the same is true with reference to *Mercurialis perennis* and *Scilla nutans*.

TABLE XV. *Average Rooting Depths of Woodland Species*

Species	Rooting depths
<i>Adoxa moschatellina</i> ...	1-3 inches
<i>Ficaria verna</i> ...	1-3
<i>Anemone nemorosa</i> ...	2-3
<i>Holcus lanatus</i> ...	3
<i>Ranunculus auricomus</i> ...	3
<i>Mercurialis perennis</i> ...	3-4
<i>Orchis mascula</i> ...	3½-4
<i>Arenaria trinerva</i> ...	4
<i>Primula acaulis</i> ...	4
<i>Sanicula europaea</i> ...	4
<i>Viola sylvestris</i> ...	4
<i>Galeobdolon luteum</i> ...	4-5
<i>Conopodium denudatum</i> ...	3-6
<i>Scilla nutans</i> ...	4-6
<i>Arum maculatum</i> ...	7-8
<i>Pteris aquilina</i> ...	6-10
<i>Rumex condylodes</i> ...	9
<i>Anthriscus sylvestris</i> ...	9
<i>Heracleum sphondylium</i> ...	12
<i>Arctium nemorosum</i> ...	18
<i>Bryonia dioica</i> ...	18
<i>Tamus communis</i> ...	18-24

TABLE XVI. *Average Heights of Aerial Shoots in May*

Species	Height of shoot
<i>Adoxa moschatellina</i> ...	1-2 inches
<i>Ficaria verna</i> ...	2-3
<i>Anemone nemorosa</i> ...	5-6
<i>Primula acaulis</i> ...	4-5
<i>Conopodium denudatum</i> ...	6
<i>Galeobdolon luteum</i> ...	7-8
<i>Mercurialis perennis</i> ...	7-9
<i>Arum maculatum</i> ...	6-10
<i>Scilla nutans</i> ...	8

(f) *The Cryptogamic Flora.* The cryptogamic flora in these woods has not been completely worked out, but appears to be distinctly poor compared with that of the *Quercus sessiliflora*-*Carpinus* woods in the same area. The Fungi are under investigation at the hands of Mr J. Ramsbottom, M.A., so

that no list is here given. Of the Mosses the following are often common: *Brachythecium rutabulum*, *Catharinea undulata*, *Dicranella heteromella*, *Eurhynchium rusciforme* often abundant on damp places, *Hypnum cupressiforme*, *Mnium hornum*, *M. undulatum* and *Thamnidium tamariscifolium*. Other frequent species are *Aulacomnium androgynum*, *Dicranum scoparium*, *Eurhynchium piliferum*, *Hypnum purum*, *H. squarrosum* (paths), *Polytrichum formosum* and *Rhynchostegium confertum*. Very few Liverworts have been noted, and of these the commonest are *Lophocolea bidentata*, *Madotheca platyphylla*, *Metzgeria furcata*, *Radula complanata*, and, on the lighter soils only, *Pellia epiphylla*. *Parmelia caperata*, *P. perlata* and *P. physodes* are the only common Lichens and the paucity of this section of the Cryptogamic flora is in marked contrast to that of the *Quercus sessiliflora*-*Carpinus* woods.

The only common Algae appear to be *Hormidium flaccidum* upon the bare patches of ground and *Chlorella* sp. and *Pleurococcus* sp. upon the tree-trunks.

(g) *Exposure*. Quite apart from the decreased intensity of the light the shade-phase is also characterised by the increase of shelter afforded to the ground-flora. The early production of foliage by woodland species involves their subjection to a very wide range of conditions affecting transpiration. The exposure is naturally greatest in the earlier months of the year, when the shelter is at a minimum. As the herbs begin to grow, however, they afford themselves mutual protection. Two features, both commonly exhibited by woodland species, tend to reduce the effect of the pre-vernal exposure. The first and most important of these is the social habit. For the shoots of any one species naturally tend to grow at approximately the same rate and to the same height. Moreover the tendency to produce their foliage horizontally at one level, an outcome of the mosaic-tendency seen in its extreme form in *Anemone* and *Adoxa*, results in a maximum of shelter. As a consequence of this each species creates its own shelter. Thus estimations of the evaporation in an uncoppiced wood showed that evaporation was 3 to 4 times as rapid above the level of the social species as in the shelter of *Anemone nemorosa* and *Mercurialis perennis*.

The second feature which tends to check excessive transpiration is the hairiness of the young leaves of many species, e.g. *Anemone nemorosa*, *Mercurialis perennis*, *Primula acaulis*, *Galeobdolon luteum*, *Potentilla fragariastrum*, *Veronica chamaedrys* and *Nepeta glechoma*. The glabrous-leaved social species, such as *Adoxa moschatellina* and *Ficaria verna*, not only inhabit the damper situations, but owing to their low growth bear their leaves in the relatively humid layer near the ground.

As the leaves of the hairy-leaved species expand, which they do but slowly, the increased rate of transpiration more or less keeps pace with the decreasing exposure. Moreover as regards internal structure the later foliage bears much the same relation to that first formed as do shade-leaves to sun-leaves.

(5) The Flora of the Coppiced Wood.

(a) *The Character of the Coppice-flora.* In most of the woods with which we are dealing the shrub layer is coppiced at more or less regular intervals. Walker in his *General View of the Agriculture of Hertford* (London, 1795) refers to its well-wooded character and states (p. 69) that "the woods are cut in succession every ten years." In a subsequent edition of the same work published in 1804 Walker mentions that the woods between Hockerill, Ware, and Buntingford are cut every twelve years when in the landlord's hands, but that tenants cut them every nine or ten years, so as to obtain the advantage of two crops in the 21 years' lease. So far as the writer's experience goes, however, many of the woods are often allowed to grow for a period of 14 to 16 years or sometimes even 20 years. By the term coppicing is implied the cutting down of the shrub layer only, though in its loose and incorrect appellation the term is sometimes employed to connote partial felling of the trees also. The two processes in practice often take place in succession, the standards being usually felled in April or May, following upon the coppicing which is carried out from January to March.

Whereas the coppicing period is relatively short the standards are only felled after 80 to 150 years, so that we must be careful to distinguish between these two causes in their separate effects.

In most of these woods the standards are too far apart to produce any very marked shading effect during the light-phase. When the leaves develop however the shading effect of the standards is pronounced. In a coppiced wood the intensity of the diffuse light during the shade-phase is usually between 20 per cent. and 40 per cent., but may be as low as 10 per cent., the differences depending upon the number of standards per acre. Where the intensity is under 10 per cent. there is no appreciable increase in the number of species as the result of coppicing, the only effect being an augmentation of the shade-flora. In such woods it is only after felling that the ground-flora exhibits the marked and rapid development which usually accompanies a cutting down of the shrub layer. The most important effect of coppicing is a greatly increased illumination and this is manifested by the vegetation in two ways. Firstly, there is a great addition to the number of species occupying the areas formerly shaded (compare Plate X, Photos. 6, 7); secondly, the species already present exhibit an increase both in the number and vigour of the individuals. A study of the lists given in Table XVI shows that the flora of a coppiced area is made up of three parts, viz. (a) the original shade-flora; (b) species formerly occupying the margins of the wood and rides; and (c) weeds. Out of 129 species recorded in the ground-flora of coppiced areas, 79 or 61.2 per cent. belong to the second category, and 38 or 29.4 per cent. are weeds characterised by the facility of their dispersal. The coppice-flora therefore tends to be abundant where the coppice-area is (1) near the

edge of the wood, (2) bordered or intersected by paths, (3) in close proximity to another area recently coppiced (see Table XVIII, *d* and *e*), (4) adjacent to cultivated ground.

Amongst the commonest species during the first season after coppicing may be mentioned *Cnicus palustris* (Plate X, Phot. 7), *Holcus lanatus* (with *H. mollis* on lighter soils), *Galeopsis tetrahit*, and *Anthoxanthum odoratum*. Other characteristic species frequent or common in the first or second year are *Melampyrum pratense*, *Agrostis alba*, *Erythraea centaurea*, *Epilobium montanum*, *Heracleum sphondylium*, *Geranium dissectum*, *Barbarea vulgaris*, *Stachys sylvatica*, *Fragaria vesca*, *Stellaria holostea*, *S. graminea* and *Poa nemoralis*. Species which pass the winter in the rosette-condition are frequent and include *Cnicus palustris*, *Dipsacus sylvestris*, *Geranium dissectum*, *Barbarea vulgaris* and *Verbascum thapsus*. The abundance of *Cnicus palustris* is illustrated by a count of the plants of this species made in a wood six months after coppicing which showed no less than 23 individuals per square foot. The maximum development of the ground-flora is usually reached in the second or third year after coppicing. Several species that were relatively subordinate in the uncoppiced state increase appreciably in amount (see Table XVII). This is very pronounced in the case of *Ajuga reptans*, *Arenaria trinerva*, *Geum urbanum*, *Galeobdolon luteum*, *Nepeta glechoma*, *Sanicula europaea*, *Veronica chamaedrys* and *Viola* spp.

TABLE XVII. *Effect of Coppicing on Frequency in Interior of Wood*

Species			Before coppicing	1st yr.	After coppicing		
					2nd yr.	3rd yr.	4th yr.
<i>Ajuga reptans</i>	f	f	c	fc	f.
<i>Arenaria trinerva</i>	vr	c	fc	o	f.
<i>Cnicus palustris</i>	absent	f	c-vc	fc-c	o.
<i>Galeopsis tetrahit</i>	absent	c-vc	o-r	o	abs.
<i>Veronica chamaedrys</i>	r	o-c	f-c	fc-r	r.

The influx of photophilous species during the first two years is illustrated by Table XVIII. As a consequence of their presence the shade-flora becomes correspondingly reduced.

TABLE XVIII. *Number of Species occupying the Interior of various Woods*

Wood			Before coppicing	After coppicing	
				1st yr.	2nd yr.
(a)	Pismire	...	9	25	51
(b)	Clapper's	...	10	35	63
(c)	Stocking's	...	10	28	65
(d)	Well Wood*	...	11	58	
(e)	Stocking's*	...	10	69	

* The coppiced areas in these two cases were adjacent to other recently coppiced areas, hence the large number of species in the first year.

The number of species in the coppiced wood increases for several years owing to the dependence of dispersal upon the time-factor. This is illustrated

by the case of Eight Acre Wood in which 34 species were present in the third year, whilst five years after coppicing the number had risen to 61. But though the number of species increases there is a decrease in the number of individuals, as the pressure of competition becomes greater. For, as the shade cast by the growing stools becomes more and more pronounced, the area occupied by the photophilous species gets gradually restricted. As a result the light-demanding species become forced further and further from the stools and thus the light-flora constitutes a sort of irregular reticulum, the meshes of which are occupied by the sprouting stools surrounded by members of the shade-enduring species. This is clearly brought out by a study of the species in coppiced woods after several years have elapsed. For example, in Cutts Green Wood out of a total of 50 herbaceous phanerogamic species present in the third year, 40 of the species were only to be found in the lighter areas where the bushes had not yet formed a closed canopy. In a second example in the fifth year after coppicing, of the 56 species 14 only were beneath the shade of the bushes. In a third wood, coppiced seven years previously, 33 out of the 46 species present were restricted to the areas beneath the interstices of the canopy. Ultimately the light-demanding species become confined, as before coppicing, to the sides of the paths and the edges of the wood.

(b) *Acidity.* I am indebted to Dr H. B. Hutchinson for estimating the soil-acidity of composite samples from coppiced and uncoppiced areas. These estimations show that the average acidity of the coppiced wood is, during the first two years, higher than that of the uncoppiced. The average acidity of the soil in the uncoppiced wood is about 0.44 per cent. whilst of the coppiced it is about 0.46 per cent. The increased acidity is doubtless due to breakdown of some of the organic matter present, since the average humus-content in the uncoppiced condition is 12.6 per cent. whereas in the coppiced it is only 10.4 per cent.

Such a decrease in humus-content entails of course a corresponding decrease in the water-content and hence greater concentration of the acids present.

It is probably in part owing to the relatively high acidity of such woods immediately after coppicing that we find *Holcus lanatus*, *Cnicus palustris* and *Anthoxanthum odoratum*, all three species characteristically tolerant of high acidities, in such abundance during the first few years. In the second or third year the acidity begins to fall and these species decrease in abundance.

(c) *Other Effects of Coppicing.* Several of the species that in the uncoppiced wood will grow in deep shade do not flower under this condition, but blossom profusely in the first year after coppicing. This is notably the case with such species as *Ajuga reptans*, *Galeobdolon luteum*, *Nepeta glechoma*, *Conopodium denudatum* and *Geum urbanum*. As already mentioned the effect in this respect is most marked upon the later-flowering species.

The increased exposure due to coppicing is expressed in the vegetation by the large number of rosette-plants already referred to. The rate of evaporation in a coppiced area may, even in the light-phase, be from 5 to 15 times that in the uncoppiced condition. The vernal species, in the first year after coppicing, often present a stunted appearance and the vigour of the vegetation in the second and third years is probably in part due to the effective shelter furnished by the sprouting stools. Probably too the power of these rosette species to kill off surrounding vegetation is in part responsible for their success.

(d) *Effect of Coppicing on Soil-temperature.* In order to obtain some idea of the effect of coppicing on the soil-temperature gradient in spring estimations were made with ordinary mercurial thermometers placed with their bulbs at the depth of maximum root-development, viz. 6 inches. To avoid any effect from direct sunlight the projecting tube was in every case covered. The temperatures were taken simultaneously in six different spots in the uncoppiced wood, and six others in the coppiced part. For purposes of comparison the average of each set has been taken. It will be seen from the accompanying table (XIX) that the temperature of the soil at this depth

TABLE XIX. *Average Soil-temperatures, Stocking's Wood*

Date	Mean temperature (° C.) of air between successive observations	Average temperature (° C.) of soil in coppiced part of wood	Average temperature (° C.) of soil in uncoppiced part
March 3		3.3	3.7 ¹
	2.7		
April 2	6.9	4.26	4.06
7	6.4	6.73	6.65
10	7.5	5.8	5.97 ¹
12	5.5	7.75	7.25
13	7.1	7.05	6.18
17	6.9	9.20	8.7
24	10.2	7.38	6.91
May 1	14.5	9.89	9.2
9	8.5	10.4	10.2
19	14.4	10.86	10.38
23		15.7	9.5
Aug. 8		15	10.5

follows more or less closely the mean air-temperature for the intervening period between successive estimations. The vernal rise in soil-temperature is clearly shown during this period, but the chief point of interest is the

¹ The higher temperature of the uncoppiced area in these two cases was probably due to shelter effect since high winds had prevailed during the intervening period.

almost uniformly higher temperature of the soil, at this depth, in the coppiced part as compared with the uncoppiced. This difference seems best explained on the ground that, the shrub layer in the uncoppiced part, by cutting off nearly 60 per cent. of the direct sunlight, greatly retards the heating up of the surface layers.

It is doubtless the upward gradient of the soil-temperature that largely determines the rate of development of the vegetation. In this connection the difference between the coppiced and uncoppiced parts is significant. For observations, over a period of years, seem to indicate that the time of flowering of the vernal species in a coppiced wood is nearly always in advance of the same species in an uncoppiced wood, and this in spite of the increased exposure. Thus, on the 20th of March, 1912, *Anemone nemorosa* was in full bloom in a coppiced wood, whereas in an adjacent uncoppiced one with no more exposure only one specimen was in bloom, whilst the remainder were in bud. The same feature was also exhibited by *Ficaria verna*.

(6) **Comparison with the Oak-Hazel Woods.**

As the oak-hazel woods of Hertfordshire have as yet been only partially worked out, the remarks here made must necessarily be of a somewhat tentative character. However, it may here be stated that the results so far obtained indicate that the oak woods with a *Corylus* shrub layer are confined to the heavier soils or on the lighter types where these are shallow so that consequently the chalk is close to the surface. As might be expected the damp societies are better represented and the following shade species appear to be more generally common: *Adoxa moschatellina*, *Ajuga reptans*, *Asperula odorata*, *Arum maculatum*, *Circaea lutetiana*, *Mercurialis perennis*, *Nepeta glechoma*, *Primula acaulis* and *Veronica montana*.

On the whole the shade-flora of the oak-hazel wood is more abundant both as to species and individuals, and this appears to be associated with a greater intensity of light during the "light-phase."

In the coppice society, *Euphorbia amygdaloides*, *Hypericum perforatum* and *Lychnis dioica* are often abundant, the last named being particularly characteristic. Amongst species of rare occurrence in the county, and which are almost or entirely confined to oak-hazel woods, may be mentioned *Dentaria bulbifera*, *Allium ursinum*, *Lathraea squamaria* and *Vinca minor*.

These few facts are sufficient to show that the oak-hornbeam is a sub-association quite distinct from the oak-hazel type in the composition of its flora. Even in the tree layer the greater prevalence of *Ulmus glabra* and *Prunus avium* in the oak-hazel woods constitutes a distinctive feature.



Phot. 1



Phot. 2

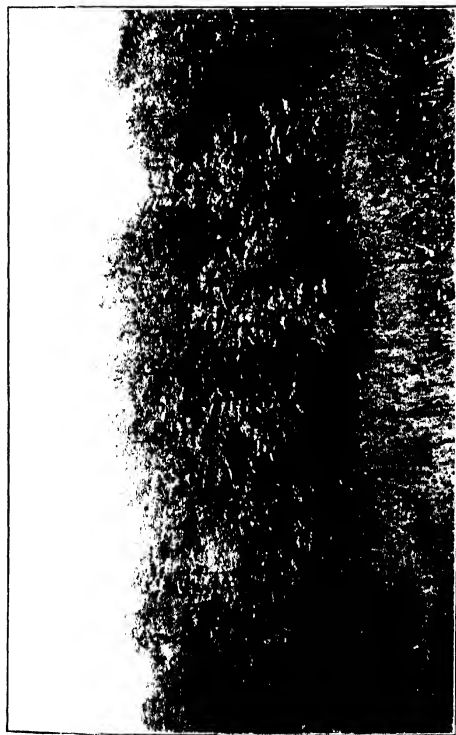


Phot. 3



Phot. 4

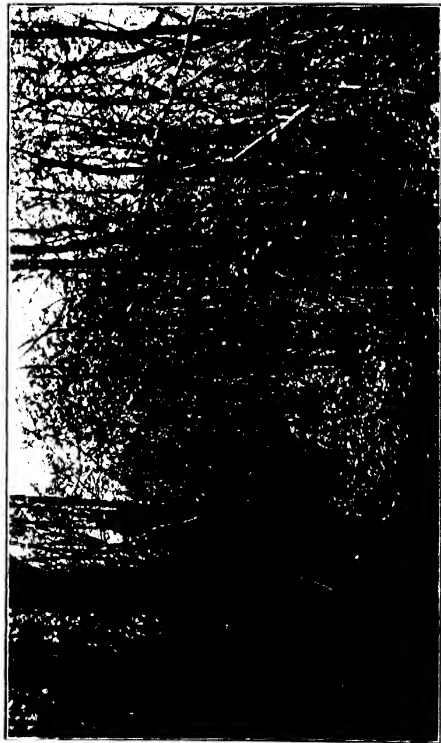
SALISBURY—OAK-HORNBEAM WOODS OF HERTFORDSHIRE (pp. 83—117).



Phot. 5



Phot. 7



Phot. 6



Phot. 8

SALISBURY—OAK-HORNBEAM WOODS OF HERTFORDSHIRE (pp. 83—117).

(7) Conclusion. Summary of Societies.

No general summary will be given here as it is proposed to epitomise the main results at the end of Part III, when comparison with the *Quercus sessiliflora*-*Carpinus* woods will be made. The chief ground societies and their relation to the undergrowth and other factors may however be conveniently summarised as under:

Shrub layer	Society	Soil factors
Carpinus	{ Pteris Anemone }	High acidity } Dry with low
Carpinus, Corylus, Sambucus...	Mercurialis	Low acidity } organic content
Carpinus and Corylus	Mercurialis	Shade } Damp } High
	Ficaria	Deep shade } Very } organic
	Ranunculus	Deep shade } damp } content
	repens	
	Marginal	Together with weeds and
	society	
	Path society }	shade-flora
		= Society of coppiced wood

DESCRIPTION OF PHOTOGRAPHS ON PLATES IX AND X

PLATE IX

- Phot. 1. *Mercurialis perennis* society, Langley Wood, occupying damp ground in portion of wood without shrub layer. Other species present are *Scilla nutans* and *Ficaria verna*. April 19th. See pp. 101 and 103.
- Phot. 2. *Anemone nemorosa* society, Stocking's Wood. Other species present are *Conopodium denudatum* and *Scilla nutans*. April 18th. See p. 101.
- Phot. 3. Mixed society, Stocking's Wood, occupying the transition region between a damp society dominated by *Mercurialis perennis* and a dry society dominated by *Anemone nemorosa*. Most of the commonest shade species are present, viz. *Ficaria verna*, *Scilla nutans*, *Anemone nemorosa*, *Conopodium denudatum*, *Arum maculatum*. Between the phanerogams can be seen *Eurhynchium rusciforma* forming an almost continuous carpet. April 18th. See p. 101.
- Phot. 4. *Ficaria verna* society, Clapper's Wood. The only other species present are *Arum maculatum* and a single shoot of *Mercurialis perennis*. March. See p. 103.

PLATE X

- Phot. 5. Rough pasture near an oak-hornbeam wood (Well Wood) colonised by numerous saplings of *Fraxinus excelsior*. To right and left are seen bushes of *Ulex europaeus*. See p. 98.
- Phot. 6. Interior of Clapper's Wood, photographed the year before coppicing, showing the very sparse ground-flora. Coppice about 16 years old. See p. 97.
- Phot. 7. Clapper's Wood, two years after coppicing, showing the abundant vegetation. Chief species present *Cnicus palustris*, *Holcus lanatus*, *Verbascum thapsus*, *Rumex condyloides* and on the right *Cnicus lanceolatus*. June 29th. See p. 112.
- Phot. 8. Stocking's Wood, one year after coppicing, showing the profusion of flowers of *Anemone nemorosa*. Compare with Plate IX, Phot 2, from same wood before coppicing. In the foreground are seen numerous tussocks of *Holcus lanatus*. April 10th. See p. 96.

NOTICES OF PUBLICATIONS OF GENERAL BEARING

ECOLOGY OF CUSHION PLANTS

Hauri, H., and Schröter, C. "Versuch einer Uebersicht der siphonogamen Polsterpflanzen." *Engler's Bot. Jahrb.*, **50** (Suppl.-Bd.), 1914, pp. 618—656, 1 text-figure.

In an earlier paper (see this JOURNAL, **1**, 1913, pp. 118–121, Fig. 8), Hauri gave a detailed description of a typical cushion plant and a brief general account of the morphological and ecological characters of plants showing this growth form. In the present paper the authors give a list of the known phanerogamic cushion plants, with further remarks on their general characters. The cushion habit occurs in 338 species, belonging to 78 genera and 34 families. An analysis of their geographical distribution shows that exactly half of the species grow in South America, especially in the Andes and the extreme south (sub-antarctic region); while the richness of the southern hemisphere in these plants is emphasised by the large number (46 species) occurring in New Zealand and Kerguelen, as well as by the number of austral genera rich in cushion-forming species (*e.g.* *Raoulia* with 20, *Azorella* with 23, *Nototriche* with 24). In Europe and Asia, each with 40 to 50 species, these plants are confined to the mountains—they are essentially plants of high altitudes and high latitudes. They are apparently very poorly represented in Africa (10 species), North America (8 species) and the Arctic (9 species). A comparison of the habitats with Warming's ecological classification shows that more than half of the known cushion plants grow where the soil is wet but acid or cold or both—as the authors point out, the distinction between "oxylophytes" and "psychrophytes" cannot be maintained. Assuming that the cushion form is a xerophilous adaptation, two explanations are open—the first the ecological view that the soil is "physiologically dry" owing to cold, to richness in humus or salt, etc., the second the historico-phylogenetic one that the xerophytic characters arose in the first instance under other environmental conditions and that the plants have persisted after these have altered. Relatively few cushion plants grow in extremely arid soils like those of deserts; a large number are characteristic of rocky and sandy substrata; while they form a marked feature in the vegetation of certain regions with a climate characterised by strong wind-action and low summer temperature. One fact that emerges from the discussion is that for all phanerogamic cushion plants, without known exception, full light exposure is an essential feature of the habitat—none grow in woodlands, and when shaded the plants lose their cushion habit or else the shaded portions die out. The typical habitat is one marked by cold and by richness in humus, as well as by wind exposure; but the authors point out that further work on the anatomy of these plants, as well as experimental investigation from the physiological side, is necessary before the various interesting questions raised by this well defined growth form can be answered.

THE CALCIFUGE CHARACTER OF FOXGLOVE

Chodat, R. "Sur la *Digitalis purpurea*, plante calcifuge." *Univ. de Genève Inst. Bot.*, Sér. 9, Fasc. 1, 1915.

Professor Chodat describes the results of certain experiments which he has performed with a view to ascertaining the nature of the effect of lime on the growth of *Digitalis purpurea*. Describing the distribution of the foxglove in Europe (it is apparently not found in a wild condition in Switzerland) Chodat refers to the generally accepted view that it is distinctly calcifuge. At the same time he points out that the ash of incinerated plants contains a considerable quantity of lime. With a view of ascertaining the exact effect of definite quantities of lime upon the growth of *Digitalis purpurea* Chodat transferred seedlings of this plant into pots of heathy soil to which had been added amounts of carbonate of lime varying from 1 to 5%. The results obtained as the photographs show demonstrate clearly the retarding effect of even 1% of lime. When basic carbonate of magnesium is added to the lime the inhibitory action is still further increased, while if dolomite, a double carbonate of lime, is added to the original soil the retarding effect upon growth is much less marked.

From these experiments Chodat concludes that the action of lime is due to its alkalinity in neutralising the acids of the humus rather than as has been suggested due to the effect of the ions Ca., for the addition of the basic carbonate of magnesium increases the inhibitory action.

Further experiments on this subject are being continued.

F. E. W.

IN MEMORIAM

Captain A. S. Marsh. It is a sad task which falls to my lot, yet deep sorrow is mingled with feelings of admiration for a life heroically laid down, and with sweet recollections of a dear friendship—the record of the life as written on the hearts of others is the true memorial.

Captain A. S. Marsh, of the 8th Somerset Light Infantry, was killed in the trenches near Armentières in January of the present year. He took his commission in his County Regiment soon after the outbreak of war, and his career in the army was but illustrative of his general ability for success when his whole energy was thrown into the work. This was due largely to a keen sense of duty rather than a real liking for military service, and there is no doubt that his experience in the study of topography and fieldcraft aided him materially in his military work. He was promoted to a lieutenancy while in training at home, and very shortly after landing in France was engaged in the terrible fighting at Loos, where his battalion suffered heavily. His promotion to command of a company and to a captaincy shortly followed.

His scholastic and university career was marked by unbroken success, and it was early evident that he was endowed with the true biological type of mind. Although a student of plant anatomy, his chief interests lay in the direction of systematic botany and the study of ecological problems. His interesting account of the work done at Holme next

the Sea was published in this JOURNAL after the outbreak of war, and having been associated with him in this work I know, alas, with what keenness he hoped to attack many problems arising out of this preliminary study. I recall incidentally a few comments of a botanical nature in his letters from France, on the abundance of *Stratiotes aloides* near their first base, as lending a martial touch to the vegetation, and a description, with sketch, of a myxomycete which was growing in the trenches.

His cheery temper, ready wit and rare choice of word and phrase will be remembered by all who knew him, and he was a keen student of English literature with a delightful bent for the discovery of the quaint and antique. Light verse was his choice in composition, and he often contributed to *Granta*, while some will perhaps recall selections of his best efforts in the *Tea Phytologist*. His favourite game was fives, and many a hard game do I recall. Besides he was a keen walker and cyclist, and naturally these pursuits were followed largely in the study of field botany. When botanical work and excursions are resumed at Cambridge his stimulating presence will be sadly missed.

It is impossible in a few words to attempt to record the many impressions and incidents which flood back to one's memory, but I trust I have done a little to keep green his memory and to make us thankful anew that England lacks not such sons to uphold her traditions.

S. R. P.

THE EMERGENCE OF THE AERIAL ORGANS IN WOODLAND PLANTS

By E. J. SALISBURY

(With seven Figures in the Text)

The general phenomenon of vernal emergence in geophytes and the morphology of the structures concerned has been dealt with by Areschoug¹ for a wide range of forms, including several woodland species. As pointed out by Areschoug the method of emergence depends on the structure of the adult condition, the stage of development of the organ at the time of emergence, and the normal depth below the surface at which the new organs develop.

The woodland flora is peculiarly suited to the study of emergence, since so large a proportion of its species are herbaceous perennials. Even those which cannot be regarded as geophytes often become covered with the fallen débris of dead leaves and twigs. To this class belong several species with a perennating rootstock whose crown is at the surface of the soil. *Primula acaulis* (Fig. 12 A), *Viola* spp. (Fig. 12 C) *Digitalis purpurea*, *Rumex condylodes* (Fig. 12 B), *Arctium* spp., *Sisymbrium alliaria* and *Geum urbanum* afford examples. In all these species the newly formed leaves push up, through any covering material, as erect structures. With the exception of *Geum urbanum*, the leaf blade is entire and its passage upwards is facilitated by the fact that the lamina is rolled or folded longitudinally so that it has a somewhat spear-like form. A second type that we may term the spear shoot is of very widespread occurrence and represented in all degrees of elaboration (see Figs. 13 and 14). The spear shoot is essentially more or less pointed but protected by one or more leaves which emerge as a result of internodal elongation. In its simplest form it is represented in the over-ground shoots of various Labiateae such as *Ajuga reptans*, *Galeobdolon luteum* and *Nepeta glechoma*, *Lysimachia nemorum*, *Veronica* spp., etc. The resistance to be overcome is in these cases but slight, the covering being, almost entirely, vegetable remains. The stem apex here is protected by two scarcely modified foliage leaves which remain small until they emerge into the light.

¹ Areschoug, F. W. C., "Beiträge zur Biologie der geophilen Pflanzen." *Lunds Univ. Arsskr.* 21, 1895.

A somewhat more specialised type is seen in plants whose shoots are often produced a little below the surface, e.g. *Epilobium montanum* (Fig. 14 B), *Asperula odorata*, *Hypericum perforatum*. Here the structure is more robust but still protected by juvenile foliage leaves. In the completely buried shoots of *Epilobium angustifolium*, *Circaea lutetiana* (Fig. 13 A), *Scrophularia nodosa* and *Bryonia dioica*, the apex is not only more pointed but in all but the last is protected by scale leaves.

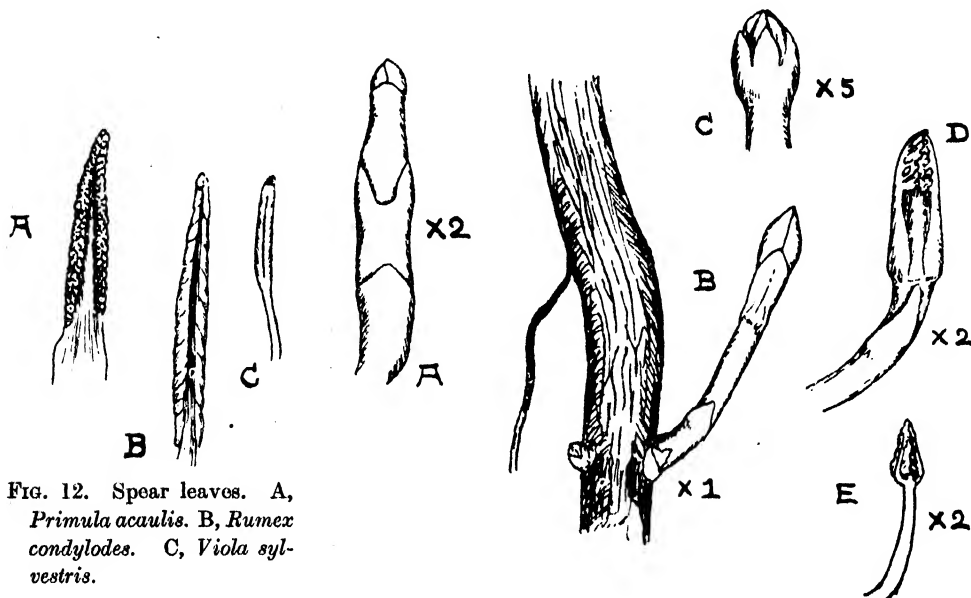


FIG. 12. Spear leaves. A, *Primula acaulis*. B, *Rumex condylodes*. C, *Viola sylvestris*.

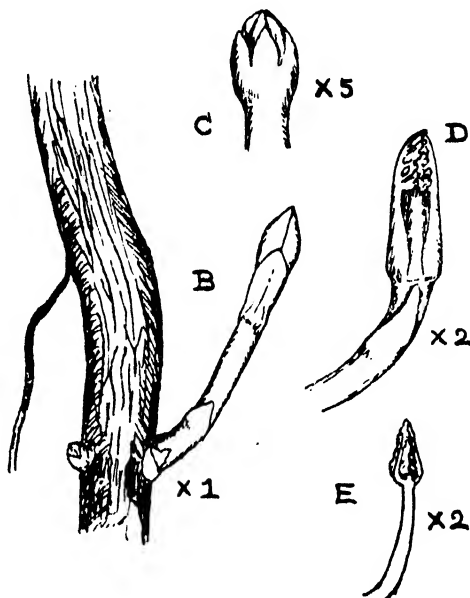


FIG. 13. Spear shoots. A, *Circaea lutetiana*. B, *Epilobium angustifolium*. C, *Asperula odorata*. D, *Stachys sylvatica*. E, *Nepeta glechoma*.

The most specialised type of spear shoot is, as might be expected, to be found in the pronounced geophytes. Amongst Dicotyledons we may note *Helleborus viridis* and *Ranunculus ficaria* (Fig. 14 A). The shoots of the former are robust pointed structures protected by scale leaves. If we examine the outermost scale leaf its apex will be found to be hard and pointed owing to the thickness of the cell walls both of the epidermis and underlying tissue. In *Ranunculus ficaria* the sheathing scale leaf is thin and membranous except at the tip where the cells have thicker walls. The apex of the pointed bud is kept rigid by the oldest leaf which is rolled parallel to the midrib and whose apex is rendered hard by the thickened epidermal walls.

The type of spear shoot met with in *R. ficaria* is with minor variations found in a large number of Monocotyledons, e.g. *Narcissus pseudo-narcissus* (Fig. 15 D), and *Scilla nutans*, *Arum maculatum*, *Polygonatum* spp., *Convallaria majalis* (Fig. 15 A and a), *Orchis* spp. (Fig. 15 C), etc. In *Narcissus pseudo-narcissus* the cell-wall of the epidermal cells at the apex of the leaf is nearly

four times the thickness at the sides and consists of a cuticle 1μ in thickness, cutinised layers 7μ and cellulose wall 12μ . In addition the outer walls of the hypoderm both here and in *Gagea lutea* are also thickened (see Fig. 16). In *Convallaria* the sheathing leaf is relatively thick at the apex and the outer epidermal walls are nearly half as thick again as upon the flanks. It is interesting to note that this essentially Monocotyledonous type is amongst investigated Dicotyledons only met with in the Ranunculaceae.

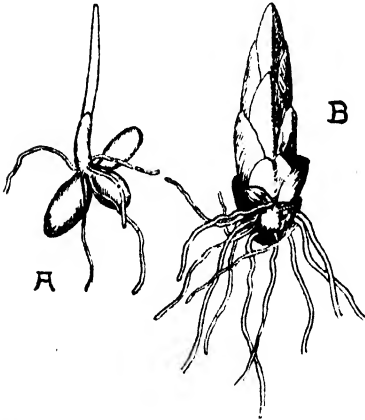


FIG. 14. Spear shoots. A, *Picaria verna*. B, *Epilobium montanum*.

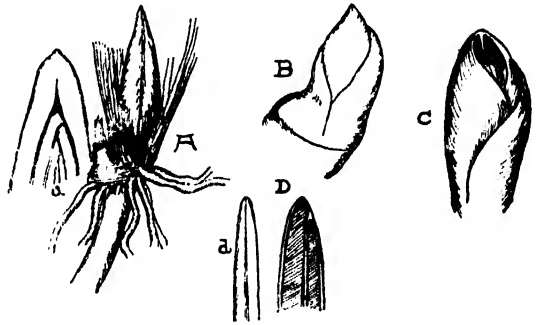


FIG. 15. Spear shoots. A and a, *Convallaria majalis*. B, *Polygonatum multiflorum*. C, *Listera ovata*. D and d, *Narcissus pseudo-narcissus*, entire and in section.

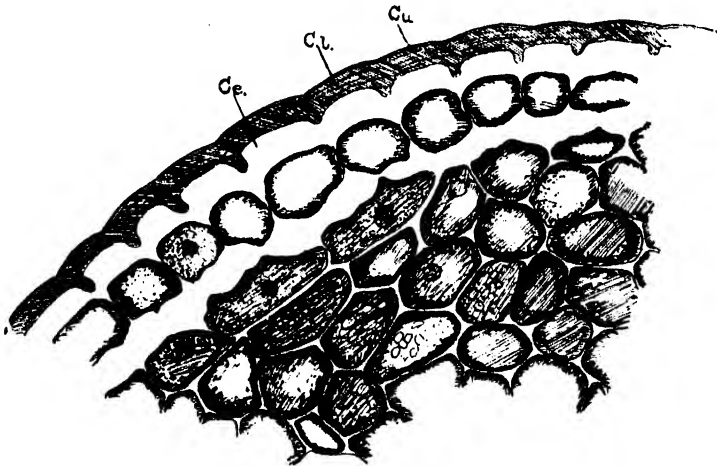


FIG. 16. Longitudinal section through a portion of the apex of a leaf of *Narcissus pseudo-narcissus*.

An important feature both of spear leaves and spear shoots, in which the leaves are rolled parallel to the midrib, is that the unfolding begins at the apex and travels downwards, the tip of the leaf or shoot thus develops an increased periphery on reaching the light whilst the basal part which has not emerged is still of small diameter. The resistance to the emergence of the remainder of the shoot or leaf is thus greatly reduced.

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The third type of emergence and also in some respects the most elaborate is that in which the stem or petiole emerges in a bent condition.

As is well known the majority of Dicotyledonous seedlings and some Monocotyledonous ones exhibit a nutation of the hypocotyl or epicotyl or, in the case of Monocotyledons, of the cotyledon itself¹. In this way the developing organ emerges without injury. On reaching the light the bent organ straightens out.

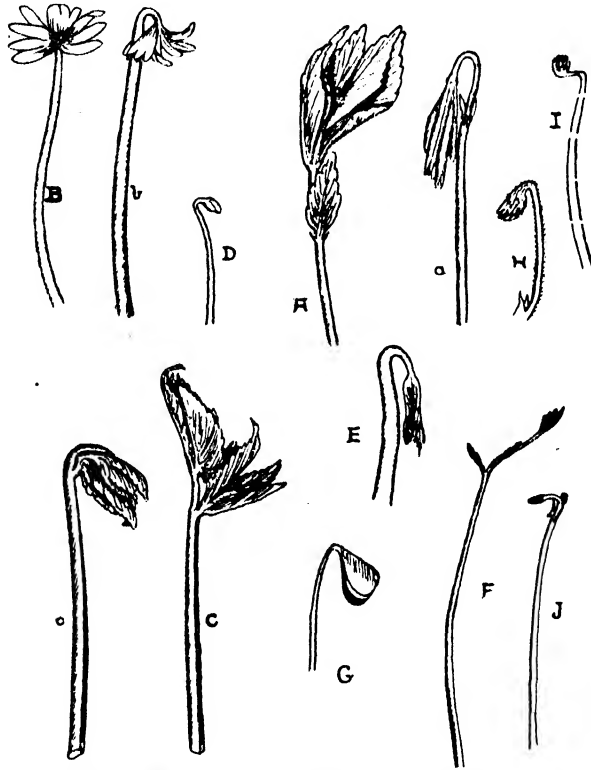


FIG. 17. Bent shoots and petioles. A, *Mercurialis perennis* grown in light, a, shoot of same age grown in darkness. B, *Eranthis hyemalis* grown in light, b in darkness—note contraction near apex. C, *Aegopodium podagraria* in light, c in darkness. D, *Ranunculus auricomus* in darkness. E, *Conopodium denudatum* in darkness. F, *Adoxa moschatellina* after prolonged growth in darkness. G, *Oxalis acetosella* in darkness. H, *Potentilla fragariastrum* in darkness. I, *Anthriscus sylvestris* in darkness. J, *Vicia sepium* in darkness.

Bent shoots and petioles may therefore probably be regarded as the retention of a juvenile character. It may perhaps be significant in this connection that the bent shoot or petiole is frequently encountered amongst members of the Archichlamydeae but appears to be relatively rare amongst the Sympetalae. Amongst woodland plants the shoots of *Mercurialis perennis* (Fig. 17 a), *Vicia sepium* (Fig. 17 J), *Lathyrus macrorrhizus* and the inflorescences of *Lathraea squamaria* and *Monotropa hypopitys* emerge as arched structures.

¹ Darwin, C., "The Power of Movement in Plants," p. 77.

Amongst Monocotyledons this feature is exhibited by *Tamus communis*.

In the hypogeal *Helleborus viridis*, although the shoot as a whole emerges as a spear shoot the inflorescence exhibits nutation. Bent petioles and stems are encountered in the following. *Adoxa moschatellina*, *Aegopodium podagraria* (Fig. 17 C), *Anemone nemorosa*, *Anthriscus sylvestris* (Fig. 17 I), *Aquilegia vulgaris*, *Conopodium denudatum* (Fig. 17 E), *Cyclamen europaeum*, *Dentaria bulbifera*, *Eranthis hyemalis* (Fig. 17 b), *Heracleum sphondylium*, *Oxalis acetosella* (Fig. 17 G), *Potentilla fragariastrum*, *Ranunculus auricomus* (Fig. 17 D), *Sanicula europaea*.

It is interesting to note that in *Ranunculus ficaria* the young plants exhibit nutation of the petiole and if the adult plant be covered over the petioles of the young leaves appear bent. In *Sanicula europaea* and *P. fragariastrum* the bent form is only assumed when the plant is covered (Fig. 17 H).

A common feature of these bent shoots, which is very pronounced in *Eranthis hyemalis* and *Conopodium denudatum*, is the more or less abrupt narrowing of the bent organ in the region of curvature. Thus in *Eranthis* the diameter in the bent region is usually about half that in the unbent. By marking the curved organ with Indian ink, in the usual manner, it can be shown that erection of the apex is brought about by a more rapid elongation of the concave as compared with the convex side, though growth on both sides takes place. The under surface of the bent region is therefore to be regarded as consisting of tissue in which the normal increase in size of the cells is retarded until the requisite stimulus is received. This is reflected both in the morphology and histology for it can be readily seen that the contraction is much more abrupt upon the under than upon the upper side. Furthermore if we cut longitudinal sections of the bent organ parallel to the plane of curvature we find that the cortex of the concave side, in *Eranthis* for example, measures some 30 per cent. less in the radial dimension than that of the convex surface. The longitudinal dimensions of a number of epidermal cells both in the convex and concave faces were measured in six different species (see Table I) and the average for all the

TABLE I. *Lengths of Epidermal Cells (averages)*

Species	Upper (convex) side	Lower (concave) side
<i>Adoxa moschatellina</i>	29 μ	18 μ
<i>Aegopodium podagraria</i>	17	12
<i>Anemone nemorosa</i>	36	17.6
<i>Eranthis hyemalis</i>	25	18
<i>Mercurialis perennis</i>	28	18.5
<i>Ranunculus auricomus</i>	36	17
Average	28.5	16.8

measurements taken showed that the epidermal cells of the upper side were usually about three-fifths the length of those comprising the upper epidermis. Moreover if we compare the average length of the epidermal cells on the respective faces the ratio between them corresponds very closely with the

ratio between the longitudinal periphery of the convex and concave surfaces. Thus in *Eranthis hyemalis* the lengths of the epidermal cells are as 1 is to 0.64 and of the peripheries 1:0.72. In *Adoxa moschatellina* the ratios were as 1:0.62 and 1:0.75, and in *Mercurialis perennis* 1:0.66 and 1:0.63. These data indicate that the straightening out of the bent tip is brought about almost entirely by the enlargement of already existing units and not by the formation of new ones.

Apart from the features just mentioned there is practically no difference between the structure of the convex and concave sides. The outer cell walls of the epidermal layer are sometimes a trifle thicker on the convex side, but this may be merely due to the enforced juvenility of the epidermal cells on the lower side. The increased thickness in *Adoxa moschatellina* must however probably be regarded as a definite protection since the outer cell walls of the convex epidermis reach a thickness of $4-5\mu$ whereas those on the concave side have an average thickness of only 1.5μ . This feature may be related to the very slender petioles of this plant compared with those of the other geophytes examined growing at a similar depth.

The following experiments show that the bent shoots and petioles of geophytes behave in a similar manner to the bent plumules of seedlings. Their chief value is that they were performed upon undisturbed plants in a wild state.

A number of developing shoots and leaves of *Mercurialis perennis*, *Adoxa moschatellina*, *Eranthis hyemalis* and *Aegopodium podagraria* were exposed by removal of the covering of soil and leaves. In each case part of the plant was covered with a cylinder of tin closed at the upper end and another part with a similar covering of glass. The shoots etc. in the dark were examined from time to time by means of artificial light. Those in the light began to straighten out in a few days but it was not found possible under the natural conditions to determine the relative sensitiveness of the different species.

The bent organs in the dark showed no change for a considerable period. After some weeks the torsion phenomenon so frequent in etiolated plants appeared in several of the specimens. In all the specimens of *Adoxa moschatellina* experimented upon, the petioles straightened out after a prolonged period in darkness. In *Eranthis*, *Mercurialis* and *Aegopodium* this same tendency was exhibited but to a much less marked degree. This peculiarity of *Adoxa* may perhaps be correlated with the fact that it usually occupies situations that are well shaded even during the "light-phase¹."

It would then appear that the absence of light inhibits the enlargement of already formed cells on the concave side, but that this inhibition is not permanent. Moreover the period of enforced juvenility would seem to vary not only in different species but even in shoots of the same individual. Shoots

¹ Salisbury, E. J., this JOURNAL, 4, 1916, p. 92.

and leaves which were encased in silver paper gave similar results, and by this means attempts were made to determine the region of perception.

A number of bent shoots of *Mercurialis* were simultaneously uncovered and their leaves were wrapped in silver paper so that only the bent portion of the stem was exposed. At the end of a fortnight all the shoots still remained bent. Where, however, a part of the foliage was left exposed to the light the curvature disappeared sooner or later according as the exposed leaf surface was large or small.

Since in a woodland most of the light, even during the spring months, that reaches the ground-flora is diffuse light relatively rich in blue rays,

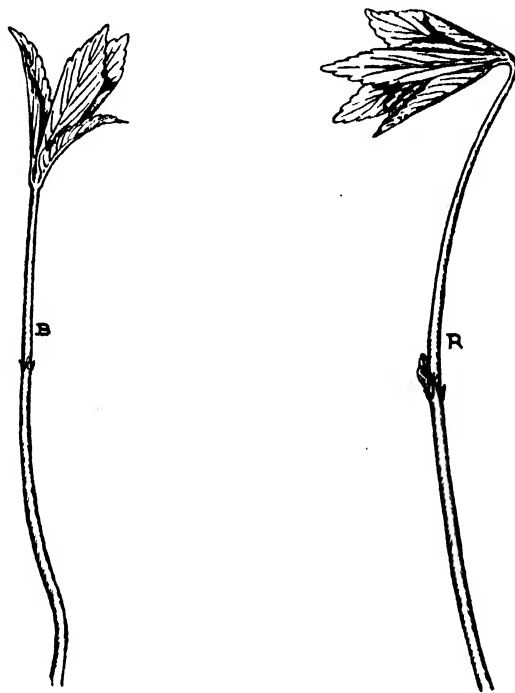


FIG. 18. Shoots of *Mercurialis* of the same age grown under red (R) and blue (B) glass.

it is of some interest to know which rays are the most effective in bringing about erection. Unfortunately there is no means of quantitatively comparing light of different wave lengths. It is, however, significant in this connection that of bent shoots of *Mercurialis* and petioles of *Aegopodium* grown respectively under blue, green and red glass, those under the blue were the first to become erect (Fig. 18) and those under the red the last. And this in spite of the apparent density of the blue glass employed.

It is clear that quite apart from the relative value of light of short or long wave length the results can only be explained as due to diminution of the effective rays accompanied by a corresponding prolongation of the reaction

period. In harmony with this it was found that under the shade of trees the response was slower than in the open. Probably here, as with phototropic response, the periods of exposure being equal, the reaction time is dependent upon the light intensity.

That darkness alone, and not the associated mechanical pressure of the soil or moisture is the inhibitory factor can be demonstrated by a slight modification of the method employed for seedlings by Pringsheim¹. The method moreover demonstrates the effectiveness of this emergence mechanism. For this purpose the shoots to be experimented upon are covered with a bank of earth so placed that the shoots lie beneath the lower edge of one face which should slope at a small angle from the vertical. The sloping face is then covered with a sheet of glass which is kept in position by means of stakes driven in at the same angle. The shoots which grow up in contact with the glass tend to straighten out, whilst still beneath the soil, and in consequence are unable to reach the surface.

Plants of *Mercurialis* and *Ranunculus ficaria* which were grown in pots in the dark showed the normal reaction to light when rotated upon the klinostat.

To summarise these results the straightening of the bent organs is a growth phenomenon which normally takes place under the stimulus of light falling upon the leaves. The brighter the light the more rapid the response, but even in the absence of light the bent structure may eventually straighten out.

¹ Pringsheim, E. G., "Reizbewegungen der Pflanzen," Jena, 1912.

AN ACCOUNT OF THE CHIEF TYPES OF VEGETATION IN SOUTH AFRICA, WITH NOTES ON THE PLANT SUCCESSION

By J. W. BEWS

(*With one Figure in the Text*)

INTRODUCTION

It seems to be an unfortunate necessity for any writer, who uses the term "formation" in connection with the study of vegetation to endeavour to define what he means by it. Plant Ecologists, however, are fairly well agreed that the term "formation" should be applied to certain natural units of the vegetation. The difference lies in the methods of determining the units. Most of the European continental ecologists including Schimper (**22**), Warming (**30**) and Drude (**12**), use "formation" to express definite physiognomic types. The British ecologists (**28**), on the other hand, emphasize the habitat as determining the formation. Since the climate of the British Isles is relatively uniform, habitat comes to be mainly a question of soil conditions and soil therefore is the master factor adhered to by the British ecologists in their system of classification. This is perfectly justifiable and in fact necessary where the climatic factors are more or less uniform.

In South Africa, however, climate is on the whole more variable than soil conditions though they both vary. To use soil as a basis of classification for South African vegetation would hardly succeed. Even in small areas climate is more important, as for instance in the Cape Peninsula, that wonderful botanical area which though only 197 square miles in extent, or a little larger than the Isle of Wight, yet, according to Bolus and Wolley-Dod's list (**6**) has no fewer than 2117 species of flowering plants. The one side of Table Mountain has Bush of the Eastern type, the other side sclerophyllous heath and Macchia. This striking difference is here certainly not due to soil conditions but to the marked difference in climate due to the S.E. mist and rain clouds. Bolus states that the annual rainfall for an average period of ten years varies between 21 and 28 inches for various stations on the N.W. side, while on the S.E. side it varies between 43 and 63 inches.

Again at Knysna no difference can be detected in the type of forest which covers the two geological formations, the Bokkeveld and Table Mountain Sandstone. In Natal, every mountain from the coast to the Drakensberg has a distinct type of vegetation on its two opposite slopes (southeastern and northwestern), depending again solely on climatic differences. The valley vegetation, too, differs from that of the higher levels, a difference however in this case depending partly on climate, partly on soil. The edaphic factors, therefore, must be recognised when necessary but the basis of any system which can apply to South Africa must be climatic. This has clearly been recognised from the first and South Africa has accordingly been divided into various botanical regions by Drege, Grisebach, Rehmen, Engler, Drude, Bolus and Marloth (15). The last mentioned author has given a series of maps illustrating the historical development of this part of the subject. The climatic factor chosen has been rainfall, but it is chiefly the floristic differences in the various regions that have hitherto been dealt with.

If we use the climatic factors as the basis of our system of classification, it becomes to a large extent physiognomic, for physiognomy is determined much more by climate than by soil conditions. At the same time, the British school have done well to emphasize the importance of habitat, though it is not only the edaphic habitat but the climatic that we have to recognise in South Africa.

At the present state of our knowledge, the units recognised as formations in South Africa are very large. Each of them has its own climatic habitat but it is not absolutely uniform nor are the types themselves. As our knowledge increases, the number of formations will also be increased. For instance I have included all the grassland without trees in one large formation, the Veld. At the same time, in former papers dealing with Natal (1, 2) I have described two very distinct types of it, High Veld and Low Veld, which, though the same species, *Anthistiria imberbis*, happens to be dominant in both, yet differ in climate, soil conditions and even in physiognomy. There are many others as distinct, e.g. the Tussock Veld of the mountain regions (3) as well as the Veld of widely separated geographical areas, such as the western region, where the toa-grass, *Aristida brevifolius*, grows in isolated tufts on the great sandy plains. All these may perfectly well be considered separate formations. Veld will then become a formation group or vegetation type. At present, however, while we are endeavouring to obtain a general, clear impression or bird's eye view of the vegetation as a whole, it is better not to enter into too great subdivision.

Cowles (9) defined three cycles of vegetative succession, as follows. (1) Regional successions "due to secular change and, in rate of development, bearing some comparison with the succession of geological periods." In South Africa, as in other countries, there has been a certain amount of more or less speculative writing on this subject but I do not propose discussing it

in the present paper. We have nothing quite so straightforward to deal with as, for instance, the post-glacial changes in the vegetation seen in North Europe and America. (2) Topographic successions "of much greater rapidity and associated with the topographical changes resulting from the activities of such agents as running water, wind, ice, gravity and vulcanism and leading generally to erosion and deposition." South Africa is an ideal country for the study of this type of succession. Where the rainfall is sufficient, as in Natal, denudation is going on with extreme rapidity and there is also rapid accumulation of deposits in certain places. The former leads to retrogression in existing stable types and the latter to progressive changes. (3) Biotic successions, where the changes are due to plant and animal agencies. "The influence of biotic agencies is not confined to areas that are characterised by a pre-erosion topography, because the interval between the periods of active erosion often is sufficiently long to permit the development of an entire biotic cycle."

Other American writers and notably Clements (7, 8) have given attention to succession. Clements has laid down certain laws of succession and the following summary gives his more important conclusions. (1) A succession results from the appearance of a new habitat or a striking change in an existing one. (2) Each stage of a succession reacts on the habitat so as to produce conditions more or less unfavourable to itself but favourable to the invaders of the next stage. (3) Initial formations are open: ultimate formations are closed. (4) The universal tendency of vegetation is towards stabilization. (5) The ultimate stage of a succession is determined by the dominant vegetation of the region. Lichen formations are often final in polar and nival zones. Grassland is the final vegetation for plains and alpine stretches and for much prairie while forest is the last stage for all mesophytic habitats. (6) The end of a succession is largely brought about by the progressive increase and competition, which makes the entrance of invaders more and more difficult.

The term "formation" is applied by Clements to stages in the plant succession. Crampton (10, 11) emphasizes the influences of the geological agents of surface change and distinguished two classes of plant formations, "Stable" and "Migratory." "The plant associations of stable formations are stabilized to the extent allowed by the prevailing climate and edaphic conditions, and are of long persistence on the same habitat, but their boundaries are subject to frequent retraction and expansion owing to the migratory nature of the habitats of the migratory formations." Stable formations resist invasion as long as climate and geographical conditions remain unchanged. In open stable formations, the physical conditions limit invasion. Migratory formations "are of comparatively short persistence on the same habitat which sooner or later undergoes change or destruction with renewal elsewhere." All the writers who have approached the subject from

this standpoint agree in seeking for causes in the geological changes, whether of major or minor character, but in addition and to a large extent dependent on the geological changes, we have climate variations often quite local and at the same time fairly extreme and in South Africa these are of considerable importance. It is this aspect of the subject which will of necessity be emphasized in this contribution.

It is, of course, quite impossible to deal exhaustively with the plant succession in a short paper such as this, and much further study will be necessary before the facts are at all adequately known. What is offered must be considered merely as tentative suggestions which may be modified and will certainly be amplified by further research. As far as Natal is concerned, details of the composition of the various plant associations referred to have been published elsewhere (1-4) and for the rest, various other works have been consulted to amplify the knowledge gained as the result of short visits paid to various parts of the sub-continent.

THE SUCCESSION ON BARE ROCK-SURFACES AND CLIFFS

A. Lithophyte Succession. In Natal, seeing that the rate of denudation is very great, there is a large development of cliffs, particularly in the Drakensberg range, where they are often several thousand feet high. There are, however, no sea-cliffs and one type of succession, therefore, common on rocky shores is eliminated. On the inland cliffs, the plant succession has only been investigated in a few localities, but probably the succession found there is more or less characteristic of them all, though of course it is to be expected that numerous minor variations will be found to occur.

The plant associations appear in the following order.

(1) *Associations of Cyanophyceae.* On the Drakensberg cliffs at the Goodoo Pass, the earliest colonist is a blue-green alga, *Glæocapsa sanguinea* Kütz. This is quickly followed by two species of *Stigonema*, a form of *S. informe* Kütz., and *S. hormoides* Born. and Flauh., the latter soon becoming more abundant and gaining the upper hand. The last arrival is *Schizothrix epiphytica*, n.sp. (Fritsch), and according to Dr Fritsch, who has kindly named the various species for me and analysed the succession, this species "has in many places almost completely enshrouded threads of the *Stigonema* with its red coiling filaments. Between the upright branches of *S. informe* and the *Schizothrix*, a struggle for supremacy is going on." The four species form an intimate association or what Fritsch (*New Phytologist*, 1906, p. 158) has called a "consortium." Similar successions were obtained from widely separated parts of the Drakensberg cliffs, e.g. at the Tugela Gorge, *Glæocapsa sanguinea* followed by the same two species of *Stigonema* and *Schizothrix epiphytica* together with *Calothrix parietina* (Naeg.) Thun. var. *africana* nov.

var. Fritsch and *Schizothrix Muelleri* Naeg. This first stage consisting of various lithophilous Cyanophyceae is exceedingly well developed in Natal. Very large areas of the cliffs are covered by it and are coloured black. In dry weather, it shrivels somewhat and peels off, restoring to some extent the original colour of the cliffs. The influence of climate on this earliest lithophilous stage is very marked. It demands warm, moist conditions and this it gets in the areas where it occurs. It has to withstand adverse conditions of drought and cold only during a comparatively short period and these adverse conditions are not so extreme on the cliffs of the Drakensberg as they are in the lower dry river-valleys. Though this stage is in general of an initial migratory nature, yet it must be considered the final stage for its own peculiar habitat, which is a very extensive one.

Turning now to the southwestern region of the Cape with its dry, hot summers we find lithophilous Cyanophyceae developed only in small patches where there is local moisture sufficient to overcome the general dry climate. I am again greatly indebted to Dr Fritsch, who has sent me the following information from samples which I collected on Table Mountain, Cape Town. The earliest colonist in this case is probably *Glæocapsa rupicola* Kütz. but the principal succeeding form is the interesting *Scytonema myochrous* (Dillw.) Ag. var. *chorographicum* W. and G. S. West. "This is the form," Dr Fritsch adds, "responsible for the so-called 'pedras negras' of Pungo andongo in Angola, where it apparently covers very considerable stretches of rock surface." Mingled with this *Scytonema* there is a good deal of *Schizothrix lardacea* Gom. which very probably formed the original base on which *Scytonema* settled down. Other species present are: *Stigonema tomentosum* Kütz. (in places the chief form growing on *Dichothrix orsiniana* Kütz. as a base), *Stigonema mamillosum* Lyngb., *Calothrix (parietina?)*, *Schizothrix* sp., *Nostoc microscopicum* Carm., *Mesotaenium violascens*, *Chroococcus turgidus*, *Navicula borealis* Ehrenb. and its variety *producta* Grun., *Zygnema ericetorum* var. *terrestre*. The occurrence of the last mentioned is interesting because it is found also on sandstone rocks in England. In one sample the main mass consisted of a new species of *Homoeothrix* which Dr Fritsch states he proposes to call *H. fusca*.

(2) *Lichen Associations*. In Natal, these are numerous but not individually extensive. They are found in drier situations than the last mentioned type and reach their best development outside the regions where summer mists prevail. The cliffs of Table Mountain, Cape Town, show a much more extensive lichen development than any of the cliffs in the eastern portion of South Africa, the climatic factors again being the determining ones. A dry, hot summer such as occurs in S. W. Cape is not favourable to the development of extensive associations of blue-green algae but does favour lichen development. Little, unfortunately, is known regarding the various species. The most abundant and characteristic in

the Cape Peninsula are, according to Marloth (15), *Parmelia conspersa*, *P. caperata*, *Physcia leucomelana*, *Pertusaria lactea*, *Umbilicaria rubiginosa*, *Xanthoria parietina*, *Trentepohlia occulta*. A species of *Pertusaria* I have often found replacing associations of Cyanophyceae.

(3) *Lithophilous Associations of Mosses and Hepatics*. This represents a distinctly new stage, which is prepared for by the previous stage or stages according to the law enunciated by Clements (vide supra). Some species, e.g. those belonging to the genera *Macromitrium*, *Brachythecium*, *Rhodobryum*, *Frullania*, *Orthotrichum*, *Fimbriaria*, etc., demand moist or fairly moist conditions, while others, e.g. species of *Grimmia*, *Dicranum*, *Campylopus*, *Andreaea*, *Brachymenium*, etc., can withstand extreme drought and strong insolation. In many places, there are wet rock flushes with ordinary green algae in great variety in addition to the mosses and hepatics. The determining factors therefore, both climatic and edaphic, are various, and strictly speaking we are dealing with separate successions. They could easily be divided on the lines indicated but to do so in this paper would lead us into too great details.

B. Chomophyte Succession. As denudation proceeds, shallow rock pans, ledges, holes and crannies appear and soil accumulates. The soil is partly derived directly from the rock itself, partly blown on or washed on to the rock surface from elsewhere. The amount and physical characters of the soil, the degree of moisture and of shade and shelter vary so that we get a variety of chomophytic types. Exposed Chomophytes, Sheltered Chomophytes, Shade Chomophytes, Hydrophilous Chomophytes, is a rough but convenient mode of classifying them. The species vary very greatly in different parts of South Africa, bearing a very obvious relationship to the surrounding formations. Lists were given for the Drakensberg in a former paper (3) and need not be repeated. They include mosses and hepatics in great variety, ferns, numerous bulbous plants, a few grasses, and in the more exposed situations, fleshy xerophytic species, *Crassulas*, *Mesembryanthemums*, etc. Many of the species are confined to this class and are never found elsewhere, but in addition there are numerous invaders from subsequent more stable types. Some of the invaders, however, never get beyond the seedling stage. All the above are migratory types. Cliffs and bare rock-surfaces give rise, by further denudation and disintegration to shingle slopes, talus or scree, and in the case of mountain tops to a special type of mountain-top detritus. The vegetation is at first chomophytic and the species are the same as occur on the cliffs. As stabilization proceeds, other species gain dominance. The climatic factors determine the ultimate stages.

FELLFIELD

The description given by Warming (30) of fellfield is as follows. "The soil is never completely covered by plants. One individual stands here and another there; between them we see bare, pebbly, stony, sandy or clayey soil, which is devoid of humus and determines the prevailing colour of the landscape." It is a description which would apply to great stretches of plant formation in South Africa, including much of the Karroo. However, even if Karroo does approximate in parts to fellfield, there is no reason why we should not retain such well-known terms as Karroo and Karroid to apply to that great region of the interior of South Africa. Outside the Karroo region, we get at higher altitudes on the Drakensberg and other mountains of the eastern side, as well as on the mountains of the southwestern and western sides, areas of typical fellfield. The first species are lithophytes and chomophytes (particularly lichens and mosses) such as have just been described. Other species growing isolated include xerophytic grasses, succulents especially Crassulaceae and Ficoideae (*Mesembryanthemum*), bulbous plants and orchids in considerable variety and sclerophyllous dwarf species of *Cliffortia*, *Erica*, *Phyllica*, *Muraltia*, *Coleonema* and various Compositae (*Euryops*, *Helichrysum*, etc.). The composition naturally varies in different parts of the country and like the chomophytic species is related to that of the surrounding formations. Probably we should include in fellfield, Marloth's "Karroide felsenheide" which is a succulent type corresponding closely with Karroo.

SCLEROPHYLLOUS FORMATIONS

The determining factors here are climatic. Sclerophyllous vegetation is characteristic of the southwestern region of the Cape, where the rainfall is mostly in winter and the summers are comparatively dry. The total amount, however, is not small, though it varies very much for different stations, exposure, etc., having a great effect. The total amount varies from about 300 to 1000 mm. (12 to 40 ins.), but Table Mountain, Cape Town, gets much more, 1592 mm. (64 ins.). Of the total rainfall, usually not more than 10 per cent. falls during the three summer months. The composition of the sclerophyllous formation of the Cape has been dealt with by numerous writers, the latest account being that of Marloth, beautifully illustrated. Details of the succession have still to be worked out. In the Cape Peninsula, the lichen associations above referred to form the earliest stage, followed by lithophilous mosses. An interesting chomophytic vegetation succeeds, including a great admixture of species. These vary with the degree of moisture available from extreme hygrophilous associations (which however are the most migratory of all) to very xerophytic types. The next stage in succession is represented in places by fellfield but generally by the Heath formation

(Marloth's "Hugelheide"). This invades the granite where the soil may be very shallow or very deep but always for several months of the year, is very dry. For full lists of species Marloth's work (15) should be consulted. The species *Blaeria ericoides* (Ericaceae) which recalls in some respects the *Calluna* of Europe is often dominant but there is always present a variety of other dwarf shrubs, e.g. *Cliffortia ruscifolia*, *Passerina filiformis*, *Sarcocolla squamosa*, *Rhus rosmarinifolia*, *Elytropappus rhinocerotis*, *Brunia nodiflora*, *Penaea mucronata*, *Leucadendron adscendens*, *Euryops abrotanifolius* and species of *Protea*, *Erica*, *Phyllica*, *Polygala*, *Muraltia*, *Aspalathus*, etc., etc.; half-shrubby or herbaceous species such as *Leonotis leonurus*, *Peucedanum galbanum*, *Cyphia bulbosa*, *C. volubilis*, *Othonna tuberosa*, *C. amplexifolia*, *Salvia africana*, *Solanum sodomaenum*, *Hydrocotyle solandra*, species of *Selago*, *Scabiosa*, *Berkheya*, *Gerbera*, *Senecio*, *Helichrysum*, etc.; Restionaceae, e.g. *Restio cuspidatus*, *Elegia juncea*, *Thamnochortus cernuus*; Cyperaceae, e.g. *Tetraria cuspidata*, *Ficinia scariosa*; grasses, e.g. *Andropogon nardus*, *Danthonia macrantha*, *Cynodon dactylon*, *Stenotaphrum glabrum*, and species of *Andropogon*, *Ehrharta* and *Aristida*; ferns, e.g. *Mohria caffrorum*, *Cheilanthes hirta*, *Ch. capensis*, *Pellaea auriculata*; and a large variety of Monocotyledons, mostly bulbous, belonging to the families Orchidaceae, Haemodraceae, Iridaceae, Amaryllidaceae and Liliaceae--*Bobartia spathacea* is one of the commonest.

This Heath formation is closed and stable, and represents the climax type for its habitat. Migratory types however occur within it where springs or "flushes" emerge. On the slopes of Table Mountain underneath the sandstone and above the granite, we get a line of such flushes. In collaboration with Dr E. P. Phillips, I hope to make a further detailed study of these and investigate more fully, at the same time, the succession in the Heath formation. So far as our preliminary investigations went there are wet flushes with *Juncus lomatoophyllus* dominant, drier flushes with the grass *Stenotaphrum glabrum* dominant, and dry or intermittent flushes with the moss *Archidium ecklonianum* dominant. The last mentioned may also represent an early stage in the Heath succession. Such flushes are conspicuous but not large. They extend for a short distance down the hillside below the point where the spring emerges. They may die out or continue as a rivulet or stream.

Along the stream-banks the type is also migratory but very characteristic, the species depending on the presence of telluric water. *Berzelia lanuginosa*, *Psoralea aphylla*, *Myrica aethiopica*, *Euryops* sp. and *Athanasia* sp. were noticed below the wet *Juncus* flush referred to above, but the stream-bank type here includes many other species, e.g. *Erica curviflora*, *Osmitopsis asteriscoides*, *Psoralea pinnata*, *P. aphylla*, *Dovea mucronata*, together with a host of smaller herbaceous forms. Moist spots on the hillside can be recognised by the dominance of such species. In fact, in a type like the

Heath formation, which includes so many shrubby species, various gradations in their water requirements might easily be recognised and the species grouped accordingly. A comparative experimental investigation into their relative transpiration rates, similar to one which I have in hand for certain Natal formations, would yield valuable information. Heath is a sclerophyllous formation in which the heaths (*Blaeria ericoides*, etc.) or heath-like forms assume dominance, and on the whole it is best perhaps to restrict the term to this type, though this hardly covers the whole of the type to which Marloth applies the term "Heide."

The **Macchia** (or **Mâquis**) is another sclerophyllous formation, much more extensive and including a variety of associations. The term Fynbosch is also applied to it locally—a term used to designate any sort of small woodland growth which does not include timber trees. Typical species belonging to Macchia include the following: *Olea verrucosa*, *Gymnosporia* (*Celastrus*) *laurina*, *Rhus glauca*, *Rhus* spp., *Myrsine africana*, *Leucadendron argenteum*, *Leucospermum conocarpum*, *Mimetes cucullata*, *Protea mellifera*, *Protea neriifolia*, *P. grandiflora* etc.; *Colpoön compressum*, *Passerina filiformis*, *Metalasia muricata*, *Cliffortia* spp., *Phylica* spp.; with Restionaceae and hundreds of other associated plants. The type however varies in different parts. Marloth's descriptions for the Macchia of Paarlberg, Tulbagh, Olifant's River and the coast region should be consulted. There are many places in which the coast Macchia shows a connection with the Karroo by the inclusion of succulents such as *Cotyledon fascicularis*, *C. cacalioides*, *Aloe* spp., succulent Pelargoniums, *Caralluma incarnata*, etc. The Eastern Macchia also shows a connection with the Eastern Bush by the inclusion of trees such as *Kiggelaria africana*, *Olinia cymosa*, *Podocarpus*, etc. At the same time, it is the climax type for its own climatic habitat.

Marloth gives details of the development of Macchia. A bare space, free from all the original vegetation, in the second year showed typical Heath formation which was gradually followed by the larger Macchia species.

The Rhenosterveld, in which the Rhenosterbosch (*Elytropappus rhinocerotis*) is dominant together with grasses, e.g. *Cynodon dactylon*, *Tristachya leucothrix* (a characteristic mountain species of the Drakensberg), *Pentaschistis airoides*, *Lasiochloa ciliaris*, *Vulpia bromoides* and a great variety of associated plants, covers large areas in the districts of Stellenbosch, Paarl, Wellington, Malmesbury, Piquetberg, Tulbagh, Ceres and Caledon, but is, as Marloth points out, not a natural but a "Kunstformation" following as a result of man's cultivation and interference (cf. the "Changed Veld" of the eastern side of South Africa).

On the flat top of Table Mountain, where the rainfall is much greater (over 60 inches), there is a more mixed type, which Marloth designates "Bergheide." This mountain Heath, however, can hardly be classed as a single formation. There are all possible gradations of water-content. The

bare exposed rock-surfaces are often covered with mats of *Campylopus atroluteus* and other xerophilous mosses. In the innumerable moist krantzies, on the other hand, the rock surfaces support an extremely hygrophilous mixture of associations. *Sphagnum* (*S. capense*) hangs in festoons and masses from the edges of dripping waterfalls. There is an endless display of leafy and thallose hepatics and hygrophilous mosses, such as *Wardia hygrometrica*, *Schistochila alata*, *Plagiochila asplenoides*, *Lepidozia laevifolia*, *Lepicolea ochroleuca*, *Jamesoniella colorata*, *Frullania diptera*, *Metzgeria furcata*, *M. nudifrons*, *Neckera pinnata*, *Aneura pinnatifida*, *Radula complanata*, *Symphogyna podophylla*, *Leucoloma zeyheri*, *Philonotis afrofontana*, *Marchantia polymorpha*, *Anthoceros punctatus*, *Fissidens fasciculatus*. Mixed with these are filmy ferns (*Trichomanes pixidiferum*). As soil gathers, there appear other ferns and flowering plants, e.g. *Acrostichum conforme*, *Todea barbara*, *Gleichenia polypodioides*, *Hymenophyllum tunbridgense*, *Cliffortia odorata*. The most beautiful of the Cape orchids (*Disa uniflora*, *D. grandiflora*) are found here. In more exposed swamps, over the flat mountain-top, various species of Restionaceae (*Restio compressus*, *Dovea mucronata*, *Elegia acuminata*, *Thamnochortus dichotomus*, etc.) are dominant with numerous other plants associated such as *Berzelia lanuginosa*, *Watsonia meriana*, *Disa graminifolia*, *Erica curviflora*, *Psoralea aphylla*, etc.

On the drier parts, the succession is entirely different, resulting in fellfield, heath or macchia. There are numerous species of *Erica* (*E. lutea*, *E. coccinea*, *E. physodes*, *E. gilva*, *E. hirtiflora*, *E. hispidula*, *E. calycina*, *E. petiveri*, *E. tenuifolia*), *Brachysiphon fucatus*, *Gnidia oppositifolia*, *G. pubescens*, *Selago serrata*, *Staavia glutinosa*, *Cliffortia ruscifolia*, *Protea cynaroides*, *P. speciosa*, *Leucadendron grandiflorum*, *L. decorum*, *Mimetes cucullata*, *Priestleya villosa*, *Aspalathus anthylloides*, *Helichrysum vestitum*, and innumerable others. Much further attention should be given to the analysis of this most interesting and complex type. The succession will be found to be partly towards the hydrophilous and mesophytic, a migratory type, depending entirely on the topography which influences for a time the climate, but mostly towards the sclerophyllous ending in Heath or Macchia as the climax type. Macchia or Fynbosch is the chief plant formation in the southwestern region, but not the only one. The coast succession there will be referred to later and the Bush, of which there is very little, will also be considered along with that of the eastern side. Macchia however is not confined to the southwestern region. It extends eastward along the mountain ranges and in the Drakensberg range bordering Natal at high altitudes, 7000–8000 feet and over, the climatic factors continue to produce a type of Macchia with *Cliffortia linearifolia*, *Myrsine africana*, *Metalasia muricata*, *Passerina filiformis*, *Erica* spp., and a variety of others. A fuller list of species I have given in a former paper (3). As we pass from the western side where the rainfall is mostly in winter to the eastern side where rain falls chiefly in

summer, the *Macchia* becomes more and more of a mountain type till in the Drakensberg, it is not found below an altitude of 7000 feet.

ALPINE OR SUB-ALPINE TYPES

The vegetation of such flat-topped mountains as Table Mountain, Cape Town, the altitude of which is less than 4000 feet, cannot be classified as alpine. It is true the climatic factors differ from those of the lower slopes, the amount of rainfall being increased, but this only tends to produce a more mixed type. On the tops of the higher mountains however, we get a true alpine type, the altitude of which increases as we proceed eastward and northward towards central Africa. The growth forms are of the usual alpine character, spreading or mat-forming dwarf shrublets, cushion-forms, rosette-forms, succulent forms, etc., many of them with large, thick, woody roots. For a list of species occurring on the higher peaks of southwestern Cape Colony, Marloth (15) may be consulted. I have also given a brief description of the "Formation of Mountain-top Detritus" as occurring on the Drakensberg at an altitude of 10,000 feet, in a former paper (3). Marloth calls the formation "Sub-alpine Felsenheide" and, in part at least, it corresponds to Warming's "Fellfield" (30).

EASTERN SCRUB

This is similar and not very far removed from *Macchia* but it is more mesophytic. It occurs in the region of summer rains and is often transitional to Forest. It does, however, in places, possess a certain degree of stability of its own. The Oudehout Scrub of the Drakensberg with *Leucosidea sericea* dominant, *Buddleia salviaefolia* frequently sub-dominant, and a number of other species such as *Myrsine africana*, *Heteromorpha arborescens*, *Cussonia spicata*, *Rhus* spp., *Royena* spp., etc. mixed—for full description see Bews (3)—is one of the best developed examples. It follows on the *Macchia* or Fynbosch of the higher altitudes and around its margins we often get sclerophyllous species such as *Cliffortia linearifolia*. Oudehout Scrub is much denser than *Macchia*, the branches of the trees interlacing, so that it is often quite impenetrable. At lower altitudes, *Rhus* spp., etc. may form similar scrub without Oudehout (*Leucosidea*). Oudehout Scrub in addition to invading *Macchia*, often colonises new ground. The *Leucosidea* itself is frequently the first species found in rocky stream channels at high altitudes on the Drakensberg. The succulent and thorny scrub with *Euphorbias*, *Aloes*, etc., of the dry river valleys at lower altitudes is of quite a different character and is best considered later.

FOREST

Bush is the term applied to High Forest in South Africa, and it is confined for the most part to the region of summer rainfall. The rainfall over the whole eastern side varies from about 25 to 45 ins. (600 to 1000 mm.) of which about 70 per cent. falls in summer. The total annual rainfall is thus not appreciably greater than in the region of sclerophyllous types, but the prevalence of summer over winter rains has a pronounced effect on the vegetation. Even within this region, however, a forest climate occurs only in certain places where the rainfall and deposition in the form of mist, protection from dry hot winds and the gradient to provide for cold-air drainage are suitable. The Bush therefore occurs only on the slopes with a southeastern aspect facing the Indian Ocean. The rest has Grassland as its climax type. The Bush may conveniently be classified into Mountain, Midland and Coast-belt types, the term Midland being taken as applying only to the region where Bush occurs and not to South Africa as a whole. Bush is quite stable within the limits of its (climatic) habitat, and as Clements points out, "forest is the last stage for all mesophytic habitats." As a result of man's interference, however, Grassland may invade the true Forest habitat, but unless prevented by the constantly recurring grass-fires Bush will re-establish itself. As forest becomes established certain progressive changes take place in the habitat. The first species are light-demanding, but they grow sufficiently close together to provide shelter for the seedlings of the more ombrophilous forest species. When these grow up they produce denser shade and the first stage disappears or retreats to the margin. Light however is only one of the factors to be considered. Temperature, particularly winter low-temperature, is of importance as helping to differentiate between Coast, Midland and Mountain types. Moisture is increased as the Bush develops and the soil characters are altered, the amount of humus increasing. The sum-total of the changes results in a more mesophytic habitat. Biological factors are also of importance in certain cases. Insects regularly destroy the seeds of certain species of trees, and in forestry practice it is difficult to obtain seedlings though plenty of seed is formed.

Our knowledge of the exact requirements of the separate species is not yet very exact, though Sim's "Forests and Forest Flora" (24) contains a large amount of information, and I am further indebted to the author for much direct assistance. Mr J. S. Henkel, now Conservator of Forests for Natal, has also kindly interested himself in the problem and has supplied me with information, as mentioned in the account which follows. At present, I can only give an outline sketch of the probable succession, which applies chiefly to Natal:

FIRST STAGE. (a) On the Drakensberg. *Leucosidea sericea*, *Greyia sutherlandi*, *Myrsine africana*, *Aloe natalensis*, *Heteromorpha arborescens*,

Arundinaria tessellata and other species included in my previous descriptions of Oudehout Scrub (3). (b) In the Midlands. Some of the above, such as *Greyia*, *Aloe* and *Heteromorpha* together with *Commiphora harveyi*, *C. caryae-folia*, *Panax gerrardi*, *Halleria lucida*, etc. (c) On the Coast. *Cussonia umbellifera*, *Commiphora* (both species), *Schmidelia monophylla* and others. All the species in the first stage are light-demanders and none of them continue after the bush closes over.

SECOND STAGE. Incursion of the more permanently leafy forms, giving a closer canopy and denser shade, and increasing the amount of moisture: *Rhus* spp., *Royena* spp., *Euclea* spp., *Celastrus* spp., and in the Midlands *Ehretia hottentotica*.

THIRD STAGE. This is, for the most part, the final stage. Under the conditions produced in the second stage, the tall forest trees grow up and commonly the yellowwood species, *Podocarpus thunbergii* and *P. elongata*, finally become dominant in the Mountain and Midland Bush, while *Rhus longifolia* and *Albizia fastigiata* are frequently dominant in the Coast Bush. The general ecological character of the Bush, as represented by this stage, is not extremely mesophytic. The species are mostly somewhat xerophilous in character, very hard-wooded and slow-growing, with hard leaves. Epiphytes are not abundant, though several interesting species occur. There is, however, a large number of lianes of the pliant, ropy or thick woody types and this increases the mesophytic nature of the Bush as a whole.

In different parts of the country, there is considerable variation in the composition. Full lists for the more important Natal forests were given in former papers (1, 2, 3) and for Cape Colony Sim (24) records the distribution of the main species. There is always a large admixture of species in every Bush and instead of yellowwood, the sneezewood (*Ptaeroxylon utile*) or the black stinkwood (*Ocotea bullata*) or the black ironwood (*Olea laurifolia*) or occasionally other species may become dominant. Further research will be necessary to explain these differences. An investigation into the transpiration rates and water requirements of the different species has been begun and it is hoped this will throw some light on the problem. Careful mapping and counting of the species on selected areas or strips will also assist us. The following will serve as an illustration. The species *Podocarpus falcata* has become completely dominant in some of the forests of East Griqualand and the Polela district in Natal. In the Insikeni Forest, E. Griqualand, a true virgin area, two acres in extent was marked out in 1900 and the increase in growth of the trees has been measured in 1903, 1906, 1908, 1913. I am indebted to Mr Henkel for supplying me with the details. The percentage composition works out as 60 per cent. *Podocarpus falcata*, 14 per cent. *P. elongata*, 19 per cent. *Ptaeroxylon utile* and 7 per cent. others. The figures, however, for trees of different diameter allow us to draw other important conclusions. Having determined the annual rate of increase, from the diameter measurements one can

gauge fairly accurately the age of the separate trees. Such a table as the following, therefore, gives a certain amount of information regarding the past history of the Bush, though conclusions in this respect must be accepted with caution, for we have no means of telling what trees have died out altogether. The table gives more definite information regarding the present regeneration and the progressiveness or retrogressiveness of the separate species. The falcate yellowwood is completely dominant and shows the best regeneration. It is ousting the common yellowwood, of which there are few young trees. Sneezewood, however, is fairly progressive, but it has not reached the size of the falcate yellowwood.

Species	Total number of trees	Diameter of stem in inches																																
		2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54						
Podocarpus falcata	140	41	18	12	10	4	8	4	2	6	5	4	2	3	4	1	1	2	3	2	2	2	1	-	1	1	1	-						
Podocarpus elongata	34	2	5	5	2	1	3	3	2	1	5	1	-	-	1	-	1	1	-	-	-	1	-	-	-	-	-	-						
Ptaeroxylon utile	48	17	3	4	4	3	3	2	1	2	-	3	3	-	2	-	-	1	-	-	-	-	-	-	-	-	-	-						
Olea laurifolia	4	1	-	-	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-						
Toddalia lanceolata	4	1	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-						
Celtis kraussiana	2	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-						
Scolopia ecklonii	2	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-						
Calodendron capense	2	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-						
Nuxia floribunda	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-						
Elaeodendron croceum	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-						

The effect of differences in the soil conditions, though not so important as climate, must not be overlooked. The majority of the forests occur on a soil derived from sandstones, sandy shales and dolerite, and is of the loose, well-aerated, high-veld type. The Ngoya Forest, however, occurs on a soil derived from metamorphic rocks (quartzites, schists, gneisses) and intrusive granite and is peculiar also in its topography. It occupies a number of minor hills and valleys in the centre of a main range. *Milletia sutherlandi* (bastard umzimbeet) is completely dominant, while the yellowwood (*Podocarpus thunbergii*) is rare. The Egossa Forest in Pondoland is derived in part from similar rocks and is of a mixed type. In the Intsubani Forest also in E. Pondoland, Sim notes again the high proportion of *Milletia sutherlandi*. Sim also points out that *Rhus erosa* and *Rhus dregeana* are present only on dolerite, that the black stinkwood (*Ocotea bullata*) is totally absent from Kaffraria while it is abundant east and west of it and that the Proteaceae are absent from calcareous soils. Such soil influences on individual species are of more importance than on the bush as a whole.

The species *Xymalos monospora* (lemonwood) deserves special mention, for it may possibly represent a fourth stage in Bush succession. It is able to survive intense shade in the seedling stage and itself at maturity has such dense foliage as to kill out all other seedlings. It withstands fire, too, and is well fitted to assume dominance, which it has done in places. It is however, limited by its water requirements, being more mesophytic than the others. This in itself indicates its place in the succession. Mr Henkel suggested to me that it may be a newcomer, and possibly this is true. Mr Sim informs

me that it extends northwards through the mountainous parts of Portuguese East Africa. It is a monotypic South African genus and the only member of the Monimiaceae found here.

In dealing with the composition of the Bush, great care must be taken to distinguish the truly virgin forests from those that have been worked. A very false picture may be presented if the percentage composition be taken of the present forests as supplied in the forestry returns. Care should be taken to ascertain what species have been felled. The composition of the Knysna forests, as given by Marloth (15) does not give a true picture of the natural composition. He gives *Olea laurifolia* as most abundant but this is simply because *Olea* has been left alone while the yellowwood has been to a large extent cut down.

After bush-fires, the succession can be easily followed. *Rubus pinnatus* is a characteristic species, almost invariably one of the first to arrive. *Xymalos*, however, if present, often survives the fire. The first growth is of herbaceous and shrubby species followed by the seedlings of the forest trees. It must not be assumed, of course, that the succession after a fire is a true topographical succession. It will naturally depend largely on the species originally present. The following list gives some of the commoner species in the early stages of the succession after fire: *Rubus pinnatus*, *Chilianthus dyssophyllus*, *Berkheya* spp., *Athanasia acerosa*, *Buddleia salviaefolia*, *Asparagus* sp., *Pteris aquilina*, *Andropogon* spp., *Solanum* spp., *Physalis* (Cape Gooseberry), *Senecio juniperinus*, etc.

In Knysna, a marked succession has been noted by Henkel (14). The species *Virgilia capensis* (keurboom), the seeds of which become widely disseminated whenever a fire occurs in the forest or the soil of the veld has been disturbed, quickly forms thickets which gradually become replaced by high forest trees growing up in the shade thus produced. Numerous instances, Henkel states, of the undoubted reclamation and extension of High Forest brought about by keur, are to be met with. It is such observations as these that we look for, from those in a position to record them.

In the Cape Peninsula, Bush replaces Macchia, as already mentioned, on the slopes of Table Mountain which face the southeast winds, and in the western forests Macchia species are often marginal to Bush, again indicating the succession.

MIGRATORY TYPES OF BUSH

Various migratory types have been recognised and described. The Stream-bank Bush of higher altitudes, with *Widdringtonia cupressoides*, *Ilex capensis*, *Ficus capensis*, *Myrsine melanophleos*, *Rhus* spp., *Erica* spp., *Myrica aethiopica*, *Aberia tristis*, *Arundinaria tessellata* and dwarfed yellowwoods, is clearly of a migratory character (3). In the same way, the Bush which fills the smaller stream valleys at various altitudes with such species as

Rauwolfia natalensis, *Trema bracteolata*, *Combretum kraussii*, *C. salicifolium*, *Celtis kraussiana*, *Rhamnus prinoides*, *Ficus natalensis*, *F. capensis*, *Voacanga thouarsii*, *Halleria lucida*, etc., is also migratory (1, 2) Ecologically these migratory types differ from the other Bush in being more open and since more light penetrates, the undergrowth of smaller shrubs and herbs (including grasses sometimes) is more luxuriant. The habitat is obviously of an unstable type.

STREAM-BANK BUSH AND SCRUB OF THE DRY INTERIOR

In the arid Karroo region and the interior and west side of South Africa generally, migratory Stream-bank Bush assumes great importance as an ecological type. Tree growth is dependent in this case entirely on the presence of the stream and river water. A fairly close connection is shown with Tree Veld and Succulent and Thorny Scrub. I am able to give a detailed description of one of the best examples of this type, through the kindness of Mr Henkel, who explored the lower Orange River Islands between Upington and Keimos. He has handed over to me a copy of the report, which he made, dated November 1908. The Orange River is the only running water present in a great tract of country and in the part explored by Mr Henkel flows over a hard rock-bed with little fall. The river, in times past, on account of the more or less level nature of the country, has divided itself into a great number of streamlets spreading over an area, varying from one-half to six miles in width. The islands, which were originally merely slight elevations, have become more prominent in course of time by the deepening of the channels between them and they have been extended by the deposition of silt. The vegetation binding the silt is of so tenacious a nature that once an island is formed, it does not readily disappear. Changes in the water level are, however, reflected in the vegetation. Along some of the courses, water has now ceased to flow, except in exceptionally heavy floods and, in such cases, the trees are dead or dying. The intensely dry atmosphere prevents rapid decay of the dead trees and there is an accumulation of dead material such as Mr Henkel has never seen before. "The effect," he says, "is extremely depressing." This illustrates very well the migratory nature of the formation. As soon as the river water is withdrawn, the vegetation dies, and it is particularly interesting to find that even when dead it holds the ground for a very long time.

Where the water is still available, a green fringing belt marks the perimeter of the islands and extends along the main banks of the river. The width of the fringe averages about 15 metres but exceptions occur, where on account of the presence of subterranean water, the width may extend to the whole island, particularly in those of more recent formation. The following were the species of trees or tall shrubs composing this Stream-bank Bush: *Salix capensis*, *Combretum erythrophyllum*, *Rhus lancea*, *R. viminalis*, *Zizyphus*

mucronata, *Royena pallens*, *Acacia horrida*, *Olea verrucosa* (in rocky places near rapids), *Tamarix articulata* (in "brak" places) and *Acacia giraffae* (in drier parts where however the soil is good, rarely near banks of the stream-lets). The species are named more or less in the order of their succession. They are all characterized by extraordinary powers of coppicing and in the case of *Royena*, of developing abundant stool shoots and root suckers. *Salix capensis* is most abundant in this place, and usually grows nearest the water. The roots are the most powerful factor in holding the loose silt and causing further deposition. The floor of this Bush is, as a rule, destitute of any growth. Regeneration from seedlings is extremely rare, except in the case of the willow, the seed of which grows freely in the wet mud on the banks. In many cases, the wide branches of the various species have been lopped for fodder for goats. Whenever this happens, fresh coppice shoots are sent out and in a few years, the shrubs are full crowned again.

Numerous references to the same type are made by almost every writer who has described the vegetation of such regions as the Karroo, S. W. Africa and the interior. In the dry river beds of the typical Karroo (the Gouph) in places *Tamarix articulata* alone is found; in other places, *Acacia horrida* (sometimes with *Viscum rotundifolium*), *Salix capensis*, *Rhus viminalis*, *Salsola aphylla*, *Atriplex halimus*, *A. nummularia*, *Lycium* spp., *Gomphocarpus fruticosus*, *Melanthus commosus* and the grasses *Aristida namaquensis*, *A. vestita*; in the western portion of the Great Karroo, *Rhus viminalis*, *Royena pubescens*, *Zizyphus mucronata*, *Phragmites communis* and *Scirpus* spp. In S. W. Africa, according to Wagner (29), the type consists of *Acacia albida*, *A. horrida*, *A. giraffae*, *Euclea pseudebenus*, *Tamarix austroafricana*, *Combretum primigenium*, *Zizyphus mucronatus*. Pearson (18, 19) in his account of his journey from the Cape to S. W. Africa, makes frequent reference to the type, mentioning as belonging to it *Tamarix* (sometimes with *Viscum*), *Acacia horrida*, *Rhus viminalis*, *Salix capensis*, *Euclea pseudebenus*, *Sisyrinchia spartea*, *Zizyphus mucronata*, *Hoodia* sp., *Rhigozum trichotomum*, *Cataphractes alexandri*, *Parkinsonia africana*, etc.

GRASSLAND

In some respects it might be considered more natural to deal with this before the Bush, since Grassland is less mesophytic and in some cases is an earlier stage in the succession to Bush. In South Africa, there is no evidence to show that this is the case. Our climate is only locally a forest climate and Grassland covers a far larger area in which it is the final stage. Indeed, as already pointed out, in many cases grassland has even invaded the true forest habitat. Forest, so far as we can trace its development, follows directly on Scrub and that on chomophytic vegetation. Grassland is not an intermediate stage. Forest and Grassland are therefore here put on an equal level, each being the final stage for its own habitat. There are, however,

intermediate types of Tree Veld to be considered later. Grass Veld may originate in the following different ways:

(a) Through the invasion by veld grasses of open or semi-open formations, formed on the soil produced as the result of the disintegration of the underlying rock. Lithophytes and chomophytes precede and sometimes Fynbosch or Heath formation forms an intermediate stage. In the typical Heath formation of the Cape, grasses are by no means absent, but they grow in tufts intermingled with other plants. In some cases, however, the grasses themselves are among the earliest arrivals. For a considerable time, the formation remains unstable. There are a large admixture of associated Veld plants; in fact it may be taken as a general rule that the more numerous these are, the further removed from complete stabilization is the Grassland formation. On the Drakensberg and other mountains, a well marked stage is represented by Tussock Veld, the alpine species of grasses (e.g. *Harpechloa capensis*, *Microchloa caffra*, *Koeleria cristata*, *Eragrostis* spp., *Anthoxanthum ecklonii*, *Tristachya leucothrix* and a variety of others) growing in more or less isolated tufts and tussocks. There is great variety of associated flowering plants present, and the type is unstable. So also on the hillsides at lower altitudes, tall species of *Andropogon* with numerous associated plants form another unstable or migratory type. The final stage is represented by large stretches of veld, where *Anthistiria imberbis* is completely dominant and the associated plants are few—a comparatively stable condition.

(b) Through soil being blown on to bare rock surfaces. The stages in the succession are essentially similar to the above.

(c) Through the invasion of river beds and the colonization of alluvial soils. The soil here is of a compact, clayey nature, badly aerated but richer in chemical salts than the loose well-aerated soil of High Veld. The pioneer grasses are species of *Aristida*, *Pennisetum*, *Setaria*, *Andropogon* and Vlei species, including numerous Cyperaceae, all representing migratory types, but the final stage is again *Anthistiria imberbis* (the distinct variety which is dominant in Low Veld).

(d) Through the silting up or drying up or draining out of Vleis and the displacement of Vlei grasses and Cyperaceae by Veld. The tall *Andropogon* species, especially tambootie grass (*A. marginatus*) and other grasses here give us an intermediate type.

(e) Occasionally by replacing Bush as indicated above. Once more the unstable *Andropogon* associations precede.

The conditions of geological stability with resulting stable plant formation only last for a time. Denudation continues and the level parts are intersected by ravines or dongas. The rapidity with which such dongas are formed and increase in size never fails to impress those making acquaintance with South African conditions for the first time. On the resulting slopes where the ground is freshly laid bare, a new succession is initiated. We

get invasion of bare rock surfaces by lithophytes and chomophytes again, and then grasses reappear, *Andropogon* and *Aristida* spp., etc., with numerous associated plants holding the ground for a time and being gradually ousted by *Anthistiria* as stabilization proceeds. Ravines, however, as pointed out above, are often taken possession of by the migratory types of Bush and if the climate, as a result of the rearranged topography, is suitable, the final stage may be Bush. There may thus be an interchange between Bush and Grassland as denudation proceeds.

There remains one notable succession in Grassland which is of a secondary nature due to man's interference and the continual burning of the grass, namely the replacement of *Anthistiria imberbis* by *Aristida junciformis*. This I have designated "Changed Veld" for want of a better term (2). Such changed veld is very extensive in parts of Natal. Other species, such as *Sporobolus indicus*, *Eragrostis curvula*, *Cynodon dactylon* are sometimes dominant in changed veld.

With increasing aridity, the typical *Anthistiria* Veld of the eastern side gives way to a semi-open type, where *Aristida brevifolius* (toa grass) grows in isolated tufts. Still more xerophytic conditions cause the almost complete disappearance of grasses and the substitution of the succulent and sclerophyllous dwarf shrubs which make up the Karroo formation.

COMPOSITAE VELD

North of the Karroo, we get a region differing from it floristically in having fewer succulents and a high proportion of Compositae. This formed one of Bolus' main floral regions—the Upper Region. Marloth calls it "Karroide Hochland." The amount of rainfall increases from west to east as does also the prevalence of summer rains over winter. Ecologically it may be considered as transitional between Karroo and Grassland. Among the Compositae in this region, the largest genera are *Senecio* (86 species), *Helichrysum* (71 species), *Othonna* (23 species), *Berkheya* (21 species), *Felicia* (17 species) [Bolus (5)]. There is, however, a fair proportion of succulents belonging to the genera *Crassula* (40 species) and *Mesembryanthemum* (23 species), and there are also Scrophulariaceae, Ficoideae, Asclepiadaceae, etc. Among the commonest species are *Pentzia globosa*, *Chrysocoma tenuifolia*, *Tripteris spinescens*, *Pteronia glomerata*, *Gazania longifolia*, *G. pinnata*, *Arctotis stoechadifolia*, *Hermannia spinosa*, *H. linearifolia*, *Aptosimum depressum*, *Mesembryanthemum nobile*, *Aloe aristata*, *Stapelia* spp., *Hoodia gordonii*, *Lycium arenicolum*, *Buphane disticha*, with a fair proportion of grasses, *Anthistiria imberbis*, *Aristida obtusa*, *Schismus fasciculatus*, etc.

VLEIS (MIGRATORY)

This is a distinctly migratory type, again comparable with the "Flushes" already referred to, in fact most of our vleis are simply flushes caused by

streams spreading themselves out over flat ground or by springs. Sometimes, however, vleis are formed in hollow rock pans or volcanic pipes and occasionally on the coast-belt as the result of silting-up. The succession is an interesting one, which I have given in a former paper (2) by classifying vleis according to wetness and degree of stagnation in the water. The first stage is represented by purely aquatic plants, various green algae together with *Nymphaea stellata*, *N. capensis*, *Utricularia* spp., *Potamogeton* spp., *Aponogeton natalense*, *Lemna*, *Callitriche*, etc. Then follows *Typha capensis* which grows in stagnant water. Next are found species of *Cyperus* (*C. latifolius*, *C. fastigiatus*, etc.) with typical vlei grasses (*Phragmites communis*, *Erianthus capensis*, *Leersia hexandra*, *Setaria aurea*, etc.), *Andropogon* spp., are mostly transitional to veld. Associated vlei plants such as *Gunnera perpensa*, *Richardia africana*, various orchids, etc., are very abundant. The above applies chiefly to Natal vleis. Marloth (15) gives a well-illustrated account of the Cape vleis. The stages are essentially similar to the above, but the species differ. *Nymphaea stellata*, *Limnanthemum thunbergianum*, *Potamogeton pusillum*, *Aponogeton distachyon*, *Oxalis natans*, *Scirpus ludwigii*, etc., form the earliest aquatic stage ("Limnäenformationen"), while *Typha*, *Phragmites*, *Prionum palmita* (Palmiet), *Richardia* (*Dantedeschia*) *aethiopica*, *Salix capensis*, *Cyperus* spp., *Cliffortia odorata*, etc., form succeeding stages of swamp—cf. also the flushes and migratory types in the Heath formation.

TREE VELD (GRASSLAND WITH SCATTERED TREES)

This is one of the most extensive of all the vegetation types in South Africa and it may be divided into several formations or sub-formations. The trees grow isolated or semi-isolated in the Veld, giving a park-like appearance. It is the Baum-Steppe of the German ecologists which we may translate as Tree Veld as far as South Africa is concerned. The following types of it occur.

1. **Acacia Veld or Thorn Veld of the Eastern side.** The soil in this case is a dry, hard, compact and badly aerated clay which is usually rich in chemical salts. The climate is dry and hot. Typical Thorn Veld occurs in the river valleys of Natal and the eastern side of South Africa generally. Thorny species of *Acacia* are dominant but other species also occur, e.g. *Celastrus buxifolius*, *Zizyphus mucronata*, *Sclerocarya caffra*, *Hippobromus alata*, *Ehretia hottentotica*, *Cussonia spicata*, *Euclea undulata*, *Chilianthus dyssophyllus*, *Nuxia floribunda*, *Rhus* spp., etc. The trees of the Thorn Veld in reaction to the adverse climatic factors, commonly assume the umbrella growth-form, with wide-spreading crowns and laterally extended root systems.

2. **Protea Veld.** The species of *Protea* composing this type prefer a loose well-aerated sandy soil, derived from sandstone or dolerite, poor in salts, especially lime. They occur at higher altitudes as on the Drakensberg

(3). *Protea roupelliae* is the most abundant there, but there are half a dozen other species. For Southern Rhodesia, Miss Gibbs (13) mentions that *P. abyssinica*, which also is common on the Drakensberg, is dominant on the "Sand Veld" near Fort Usher. Soil conditions are undoubtedly of importance in determining this type.

3. **Bush Veld.** This is the term applied to Tree Veld in the Northern and Northeastern Transvaal. It may be described as a Combretaceous-Leguminous type, the characteristic species being *Terminalia sericea*, *Combretum apiculatum*, *Burkea africana*, *Peltophorum africanum*, *Ficus cordata*, *F. capensis* and *Faurea saligna*, with occasional Acacias, *Cussonia spicata*, etc. Tree ferns (*Cyathea dregei*) grow to a large size near water. The presence of Aloes and Euphorbias, with species of *Mesembryanthemum*, *Kalanchoe*, *Stapelia*, *Anacampseros*, etc., on dry rocky hillsides indicates a connection between Bush Veld and succulent types to be considered later—Succulent Scrub and Karroo.

4. North of the Witwatersrand, according to Marloth (15), *Dombeya densiflora*, *Croton gratissimum*, *Chrysophyllum magalismontanum*, *Barbacenia retinervis*, *Cissus* spp. and *Protea hirta* form a distinct type, showing connection with Tree Veld of the interior.

5. In the Tree Veld of Rhodesia, south of the Zambesi, Miss Gibbs (13) states that *Combretum terminalia*, *Bauhinia* and *Sterculia* spp. with *Azelia cuanzensis*, *Peltophorum africanum*, *Copaifera coleosperma* and *Adansonia digitata* (baobab) are the commonest. She also notes the presence of *Oncoba spinosa*, *Ximenia caffra*, *Diplorrhynchus mossambicensis*, *Royena pallens*, *Olex dissitiflora*, *Bolusanthus speciosus*, and *Vitex flavescens*. "Tree Veld appears to be the vegetative type for the whole country."

6. The Western Transvaal, Bechuanaland and the central plateau of S. W. Africa are all either Veld or Tree Veld, with bare waste tracts becoming increasingly arid towards the west. The Bush Veld gives way to Thorn Veld and that in turn to semi-desert in places. According to Sim (24) a large proportion of the former timber vegetation of this region consisted of the large Camelthorn (*Acacia giraffae*), *Acacia detinens* and *Olea verrucosa* with *Acacia horrida* near streams and springs but within a hundred miles of Kimberley those have now mostly disappeared, being used up for firewood.

In S. W. Africa, the toa grass (*Aristida brevifolia*) covers large areas of Great Namaqualand with the trees *Acacia giraffae*, *A. detinens*, *Aloe dichotoma*, *Boscia foetida*, *Rhigozum trichotomum*. Northward in Damaraland, *Acacia albida*, *Acacia* spp., *Albizzia anthelmintheca*, *Boscia pechuelii*, *Dichrostachys nutans* and *Euphorbia* spp. Schinz (23) calls the eastern edge of Namib desert, which will be referred to later, "Euphorbia Steppe." The Tree Veld of this region, like that of the Transvaal, becomes more mesophytic as we proceed eastward. Still further north, according to Wagner (29) "east, and south-east of the Otavi Range, the plains have the character of gently

undulating expanses of tree steppe, the aspect of which is rendered distinctly tropical by the presence of tall, graceful palms (*Hyphaene ventricosa*). To the north and north-east of the range, they are, for the most part, covered with open forest, interspersed in the vicinity of Omuramba Ovambo with glades of delightful park land." The stream-bank types of S. W. Africa have already been dealt with.

7. Still further north in Angola, Pearson (18, 19) describes types in which *Copaifera mopane* is the dominant tree. The undergrowth, he says, is very rich in grasses, also including Pedalineae, Oldenlandieae, *Monsonia*, Acanthaceae, Capparidaceae and Leguminosae. Evidently it is a mesophytic type, not far removed from true forest, into which it passes. Pearson also notes the presence of Acacia Veld and Baobab Veld in this region. So far as can be judged it appears similar to the Rhodesian and eastern regions of the same latitude. The above types are all ecologically distinct but the arrangement given is a purely geographical one. Tree Veld can be subdivided ecologically into at least the following types: (1) *Euphorbia* Veld, (2) Acacia Veld, (3) *Protea* Veld, (4) *Terminalia* Veld (Leguminous Combretaceous type or Bush Veld), (5) Baobab Veld, (6) *Copaifera* Veld. These are named roughly in the order of increasing mesophytism, but doubtless there are others and much further attention should be given to determining the requirements of the various species. The more xerophytic types mentioned connect with Succulent and Thorny Scrub.

Tree Veld covers an enormous area in South Africa extending as it does from Portuguese East Africa right across Rhodesia, the Northern Transvaal, Bechuanaland and S. W. Africa to the Namib. It extends northwards along the coast to the Congo and much of Central and Eastern Africa is of the same type. It fills all the dry river valleys of the south-east side except in places where Succulent Scrub occurs. Its ecological history and significance is therefore of great importance. It is obviously intermediate between Grass Veld of the ordinary type without trees and Close-bush or Forest. Two views are possible regarding its origin. First it may be regarded as the remnants of a previous closer type of bush, which has become retrogressive either through a change in climate or owing to the influence of grass-fires. This view is commonly supported, but it involves certain difficulties. Grass-fires presuppose the presence of grass, and therefore could hardly have been a factor which would lead to a change from Bush to Tree Veld, since grass was not present in the former. Nor is there any real evidence of any pronounced change of climate, sufficient at any rate to explain the very great effect on the vegetation. The species in the Tree Veld are all light-demanders and could not have existed in dense Bush. It would be necessary to suppose, therefore, that the previous Bush species have entirely disappeared from those great areas and have been replaced by the other species at present found there. The present type must have existed for a very long time, for the

various types of mammals (springbok, etc.) are not adapted to forest conditions and they are extremely numerous in point of species.

The other view is to regard the Tree Veld as the initial stage in a Bush succession. The grass-fires prevent the trees from growing closer, and thus the present condition of things is maintained. In the Thorn Veld, where grass-fires are prevented by heavy grazing or by other means as when an area is fenced in and protected, the thorn trees and other species tend to close in and form thorn thickets. Clumps of *Acacias*, *Celastrus buxifolius* with *Royena* spp., etc. commonly occur even in the ordinary Thorn Veld. A second stage is represented by a closer growth with various lianes growing up in the thickets and increasing the shade. Various ferns appear in the undergrowth which becomes denser. The progression is towards the mesophytic. Were grass-fires entirely prevented, the succession would be limited only by the climatic factors. These at present are of too adverse a character to permit of high forest and it is impossible to say how far the climate would be altered by the presence of denser vegetation or how far the type would progress in the absence of fires. The different varieties of Tree Veld depend on differences, partly in climate, partly in soil conditions and partly it may be, since the area covered is so great, on the factors controlling the distribution of species, some of which may be no longer in operation.

SUCCULENT AND THORNY OR SEMI-KARROID SCRUB OF LOWER ALTITUDES

This type is found in Natal in the dry river valleys, e.g. the great valley of the Tugela. It shows connections with the more xerophytic Tree Veld but differs in being more dense and in the relative scarcity of grasses. In Natal, it consists of tree *Euphorbias* (*E. tirucalli*, *E. grandidens*), *Aloe* spp., *Encephalartos allensteinii* (in places), *Commiphora* spp., *Hippobromus alata*, *Rhus* spp., *Ptaeroxylon utile*, *Acacia* spp., *Mesembryanthemum* spp., with succulent or semi-succulent lianes such as *Sarcostemma viminalis*, *Dregia floribunda*, *Riocreuxia* sp., *Capparis* spp., *Secamone* sp., *Ceropegia*, *Vitis* spp., *Senecio* spp., etc. Outside Natal it occupies still greater areas. Westward, from the Kreiskama River and particularly in the district of the lower Fish River, a similar type is described by Sim (see p. 5 of "Forest Flora"). In addition to succulents, there are present in this case very much dwarfed forest species such as *Ptaeroxylon utile*, *Elaeodendron croceum*, *Apodytes dimidiata*, *Scolopia zeyheri*, *Sideroxylon inerme*, *Celastrus peduncularis*, *Schotia latifolia*, as well as others more characteristic of Succulent Scrub, *Portulacaria afra*, *Capparis albitrunca*, *Maerua triphylla*, *Pappea capensis*, *Euclea undulata*, *Olea verrucosa*, *Rhus* spp., *Royena* spp., *Celastrus* spp., *Euphorbia* spp.

According to Sim, "The shrub trees grow in clumps or thickets separated everywhere by bare paths or water runs. Viewed from an overlooking

height, the landscape shows a vast, flat, forest plain apparently dense and of unknown depth as the interspaces only show on close inspection, but a closer inspection shows that it is rather a goat-grazing country and an ostrich run than a timber forest. When the spekboom (*Portulacaria*) is in flower, its bright rosy colour pervades the scene; at all other times the landscape is dull and sombre, desolate and monotonous, the secluded resort of the koodoo, the buffalo, and the elephant." Somewhat the same class of scrub, Sim states, extends interruptedly as far up as Witmos and Bethesda, and it extends also through the Addo Bush to beyond Uitenhage. It is replaced by Thorn Veld along the river valleys above Cradock. Towards the Kat River and upper Keiskama streams, the Fish River scrub gradually merges through rather poor sneezewood and wild olive scrub into high forests of the Amatolas.

The ecological nature of this type was recognised by Sim, when he says, "Fish River Scrub is the effect of a Karroo climate on a forest vegetation." Once more, it is obvious that it represents the final phase for its own climatic habitat like sclerophyllous Fynbosch, *Leucosidea* scrub of the Drakensberg, etc. With more mesophytic climatic conditions it grades into Bush.

It is necessary here to explain why this type was not considered along with the sclerophyllous types. At first that was my intention but on reconsideration it was thought inadvisable to make it appear that the succession has always been towards the mesophytic. Succulent Scrub is essentially a valley or at least low-lying type, contrasting thus with *Leucosidea* scrub, which is a mountain type. Though it grades into Bush, there is no reason in the absence of direct evidence why it should be considered a stage in Bush succession. Retrogressive Bush might just as well be considered a stage in the Scrub succession. It cannot be too much emphasized that each is the final phase for its own habitat.

THE KARROO

This succulent and sclerophyllous dwarf-shrub type represents the effect of a dry, continental climate on Grassland. The Karroo region consists of a great, shallow basin varying in its altitude from 1800 to 2500 feet above sea level, surrounded by mountains from 4000 to 8000 feet high. The rainfall varies greatly. In the driest parts (the Gouph) it is from 3 to 6 ins. (81-150 mm.) but the Little Karroo has a higher rainfall, 5 to 14 ins. (136-354 mm.). The greater part of the rainfall takes place in the summer months. The summers are very hot and the winters cold. The soil, largely in reaction to the dry, continental type of climate, is rich in chemical salts but very dry and baked. There is seldom any water in any of the numerous stream channels.

Ecologically, Karroo is, for the most part, an open or semi-open formation but nevertheless it should be classed as veld or steppe rather than as desert, for annuals (therophytes) though they occur are not very abundant or

characteristic (vide later in the description of desert). The best general description of the Karroo that has appeared so far is that of Marloth (15). His excellent photographs and drawings give a good idea of the many weird growth-forms.

The Gouph (a Hottentot word, meaning empty, bald, naked or nothing) may be taken as the most typical Karroo formation. Marloth classifies the most important species according to their growth-forms as follows. (a) *Bushes and dwarf shrubs* such as *Lycium arenicolum*, *Rhigozum trichotomum*, *Pelargonium* spp., *Zygophyllum* spp., *Astephanus massonii*, *Hermannia desertorum*, *Dicoma diacanthoides* and other Compositae, *Carissa arduina* with *Viscum rotundifolium*, *Pentzia virgata*, *Walafrida geniculata*, *Galenia africana*, *Diplopappus filifolius*, *Chrysocoma tenuifolia*, *Relhania genistifolia*, *Hibiscus urens*. What is most striking is the almost total absence of green colour. "Braun ist die Farbe der Karroo." Most of the species have large root systems. (b) *Leaf succulents*, including a large number of species of *Mesembryanthemum* and *Crassula*, *Anacampseros*, *Augea capensis*, *Sarcocaulon patersonii*, *Aloe* spp., *Haworthia margaritifera*, *Gasteria disticha*, *Apicra deltoidea*. (c) *Stem succulents*, e.g. *Cotyledon fascicularis*, *Euphorbia* spp., *Stapelia* spp., *Caralluma* spp., *Hoodia gordonii*, *Trichocaulon piliferum*, *Senecio* spp., *Kleinia* spp. (d) *Plants with underground water storage*, e.g. *Asparagus* sp., *Fockea* sp., *Pachypodium bispinosum*. (e) *Bulbous monocotyledons* belonging to the orders Iridaceae, Amaryllidaceae, Liliaceae (e.g. *Buphane disticha*). (f) *Grasses*: tufts of *Aristida obtusa*. (g) *Annuals*: *Arctotis stoechadifolia* and other Compositae, *Citrallus vulgaris*; species of *Helichrysum*, *Senecio*, *Sphenogyne* and *Cenia*.

The western portion of the Great Karroo is similar in many respects to the Gouph, but contains an admixture of rhenosterbosch (*Elytropappus rhinocerotus*) and ferns (*Pellaea auriculata*, *Cheilanthes pteroides*, *Ch. induta*). In the eastern Karroo, the flats are again typical of the formation while the hills have *Aloe ferox*, *Pappea capensis*, *Carissa arduina*, *Capparis oleoides*, *Rhigozum trichotomum*, *Portulacaria*, *Encephalartos* spp., *Testudinaria elephantipes*, showing a connection with Succulent Scrub. There are also outposts of sclerophyllous, south-western vegetation, and on the higher mountains eastern types like *Kiggelaria africana*, *Buddleia salviaefolia* and *Cussonia spicata*.

In the Little Karroo, there are taller Crassulaceae, e.g. *Cotyledon fascicularis*, and over wide stretches the guarri (*Euclea undulata*) is dominant. The Touws River region shows an admixture of sclerophyllous Cape species, e.g. *Protea*, *Leucadendron*, *Erica*, *Phylica*, *Thamnochortus*, *Willdenowia*. The Robertson Karroo is a low-lying isolated patch of Karroo, surrounded by sclerophyllous formations. The West Karroo (Bokkeveld and Roggeveld or Tanqua Karroo) is also partly typical Karroo formation but shows transitions to the Cape region.

The migratory stream-bank vegetation of the Karroo region has already been dealt with. It was also pointed out that the Fellfield, which occurs in various other regions in South Africa approaches very near to Karroo formation. In Natal, in certain places, as for instance in the valley of the Tugela below Weenen, there are bare rocky slopes with succulent and hard shrubs which might be classed as Karroo.

There is room for much further work on this interesting type. The plant succession is still unknown to us. Transitions have been noted in the above account between Karroo and sclerophyllous woodland on the western side, between Karroo and Thorny and Succulent Scrub on the southern and eastern sides. On the north, Karroo passes into Compositae Veld which it approaches in its ecological character and through it into Veld. . On the eastern side, it also grades into ordinary Veld. The edaphic factors are undoubtedly of importance as well as the climatic. Not only is the soil dry, hard clay but the relatively high proportion of chemical salts, it may be suggested, may possibly be one of the main factors which determine the prevalence of the succulent habit.

"BRAK" FORMATION

Over all the arid portions of South Africa, such as the dry river valleys of the eastern side and the whole Karroo and western and central portions, the soil is, as a rule, rich in chemical salts. This is a direct result of the dry climate. Precipitation is not sufficient to leach the soil and salts accumulate. In low-lying places, there is a certain amount of seepage and subsequent evaporation leads to the formation of salt pans. The vegetation of these is distinct enough in point of both habitat and physiognomy to constitute a separate formation. *Tamarix articulata* is characteristic of such places and various halophytes such as *Salsola aphylla* (Gannabush), *S. zeyheri*, *Atriplex halimus*, *Lycium* spp., *Statice* sp. etc. Pearson (18, 19) makes repeated mention of such halophytic associations for the western region, and towards the north, salt pans, according to the maps, occupy large areas. The detailed study of this formation appears to offer an attractive field.

DESERT

If we classify Karroo along with Veld, there is not a very great area of actual desert anywhere in South Africa. Raunkiaer (20, 21) and other Danish botanists, as Ove Paulsen in his memoir on the vegetation of the Transcaspiian Lowlands (17), use as a test for desert, the high proportion of annuals (therophytes). In the Libyan desert this, according to Raunkiaer, is 42 per cent. while the normal for the whole world's flora is given as 13 per cent. Annuals, however, are also characteristic of regions under high cultivation where the soil is continually disturbed. In a previous paper I have shown that Natal has only 6-7 per cent. of annuals and many of these are doubtfully native. This

is only about half the normal. The other formations already described also are poor in annuals so that if we apply this test none of them can be classed as desert. The so-called Kalahari desert is to be classified not as desert, but Veld. The Namib desert in S. W. Africa is, however, probably true desert, as I am informed by Dr Pearson that the proportion of annuals in parts of it at least is relatively high. Pearson (18, 19) has made a special study of this region, and it is largely due to his researches that its flora is now becoming fairly well known. He looks upon the flora as being derived from each of the surrounding plant formations. During his last visit, he made some extremely interesting notes on the plant succession which will be included in a forthcoming paper.

Marloth visited the Lower Namib in 1909 and in his description of the vegetation (16) he distinguishes four edaphic formations—seashore, sandy plain, rocky hills and gravel-covered flats. *Salsola zeyheri*, *Acanthosicyos horrida*, *Mesembryanthemum* spp. are characteristic of the sandy plains to the south, while to the north is the well-known *Welwitschia*. On the rocky hills, the kokerboom, *Aloe dichotoma*, and several species of *Euphorbia* (*E. gummi-fera*, *E. cervicornis*), *Pteronia succulenta*, *Pituranthus aphyllus*, *Mesembryanthemum rhopalophyllum*, *Augea capensis*, *Sarcocaulon rigidum* (Bushman's candle). The central plateau, as already described, is an arid type of Tree Veld.

THE PLANT SUCCESSION ON THE COAST

The whole coast-line of South Africa except in a very few places is sandy, and the drifting sand, by invading the other formations, has produced an entirely new succession which is fairly easily determined. The sand-dunes which line the eastern side vary in height from 50 to 200 feet and have been entirely fixed by the growth of Psammophilous Bush.

In Natal, the succession is as follows. On the belt of shifting sand between the bush and the sea the following species grow and act as sand-binders: *Scaevola lobelia*, *Cyperus natalensis* (the leafy form), *Ipomaea pescaprae* (*I. biloba*), *Hydrophylax carnosa*, *Gazania uniflora*, *Mesembryanthemum edule* and the grass *Sporobolus pungens*. The actual order in succession between these varies at different spots. As soon as the sand gets partially fixed, a variety of other species come in, e.g. *Canavalea obtusifolia*, *Cryptostemma niveum*, *Passerina ericoides*, *Helichrysum teretifolium*, *Osteospermum moniliferum*, *Samolus porosus*, *Tephrosia canescens*, *Cynanchium* spp., *Brachylaena discolor*. Then follows the typical Sand-dune Bush with *Mimusops caffra* (red milkwood) dominant and a great variety of other trees such as *Scolopia zeyheri*, *Brachylaena elliptica*, *Erythrina caffra*, *Apodytes dimidiata*, *Kraussia lanceolata*, *Dovyalis rotundifolia*, *Rhus* spp., and in places *Strelitzia angusta*, *Hyphaene crinita*, *Aloe supra-laevis* and *Strychnos spinosa*. The abundance of lianes is a feature of Sand-dune Bush, while herbaceous undergrowth is

almost entirely absent. The trees composing the Sand-dune Bush are on the whole very distinct from the species found in the Coast Bush behind the dunes, though some of the sand-dune species occur at higher altitudes.

Psammophilous tree-growth is confined to the eastern coast where the climatic factors permit of it. At the Cape, the succession is different. Marloth (15) figures *Myrica cordifolia*, *Chymococca empetroides*, *Passerina filiformis* and *Sideroxylon inerme* as "Dünensträucher" and in one of his excellent plates shows the grass *Ehrharta geniculata* binding the sand, followed by *Mundia spinosa*, *Myrica cordifolia* and on the summit of the dunes, *Rhus crenata*. The more adverse climate of the Cape has the same effect on the sand-dune vegetation as on the other types. Instead of tree-growth we get a type corresponding to Sclerophyllous Woodland.

At the river mouths, the succession differs. In wet sandy soil where the water is not brackish we get, instead of the Sand-dune Bush, the interesting *Barringtonia racemosa*, *Hibiscus tiliaceus*, *Voacanga thousarii*, *Eugenia cordata*, etc. On mud flats at the river mouths with salt or brackish water, various halophilous species such as *Salicornia* and *Chenolea diffusa* form spreading clumps. As far south as the rivers of the Transkei (Kogha River mouth) the final stage on the mud flats is Mangrove formation. The three species of Mangrove found at Durban are *Rhizophora mucronata*, *Bruguiera gymnorhiza* and *Avicennia officinalis*. Mangrove formation increases enormously in importance as we proceed northwards along the coast of Portuguese East Africa. Sim (25, 26) states that it lines, with interruptions, the whole coast of that region from Delagoa Bay northwards and extends inland along the rivers for many miles. In addition to the more hardy species which form outliers in South Africa named above, the following occur: *Ceriops candolliana*, *Carapa moluccensis* (*Xylocarpus granatum*), *Lumnitzera racemosa*, *Sonneratia acida*, *Heritiera littoralis* with the fern *Acrostichum aureum* as an occasional companion.

GENERAL REMARKS

There are few countries that can show more varied types of vegetation than South Africa. There is every stage from desert and open edaphic formations, through every gradation of open, semi-open and closed Steppe, through great variety of sclerophyllous and other Scrub to a mesophytic type of Evergreen Bush, while along the coast, there are Psammophilous Bush and Mangrove types. The succession is not always towards the mesophytic as is shown by the presence of Succulent Scrub in the dry river valleys. Tree Veld of various kinds—an intermediate type between Grassland and Forest—covers enormous areas and may represent an early stage of succession to a xerophytic type of bush, which retains its present character through the influence of grass-fires.

One striking feature of the vegetation as a whole is the rarity of formations

or associations dominated by a single species. The Macchia and Heath formations, Scrub of various kinds, most of the Bush, much of the Veld and Tree Veld, the Karroo and Psammophilous Bush of the coast, are all made up of a conglomeration of species. In the closer formations masses and clumps or tussocks, consisting of half a dozen species with their branches completely intertwined and commingled are a common feature. There are, however, a few exceptions to this. In parts of the Karroo, a single species such as *Rhigozum trichotomum* or *Mesembryanthemum spinosum* may be completely dominant over a considerable area. *Anthistiria imberbis* forms pure associations over much of the Veld, and other grasses such as *Aristida* spp. are also often dominant. *Leucosidea* scrub in the Drakensberg is sometimes fairly pure, and there are a few examples of almost pure *Podocarpus falcata* bush. Parts of the Thorn Veld, too, have no other trees than Acacias.

In many cases, the fact that no single species has been able to assume dominance may be considered to point to a lack of stability in the environmental conditions, but it is doubtful if this is sufficient to explain all the facts. *Leucosidea* scrub is an unstable type and yet it is often pure. The wattle tree, *Acacia mollissima*, a native of Australia, large plantations of which are now a feature of the landscape in Natal, is quite at home and in places, e.g. in the Harding district, is spreading naturally. Among the wattle, hardly any native species is able to exist. There is no undergrowth of any kind. An introduced species therefore is apparently able to assume complete dominance, while our native species of trees are not. This, however, is not apparent in the case of introduced weeds, with one or two exceptions. The vegetation of South Africa, as a whole, is resistant to invaders. The relationship between the various types of vegetation as described above is indicated in the accompanying diagram (Fig. 19). It is meant to apply however as a whole, only to the eastern side of South Africa.

In conclusion, it is hardly necessary to state what must be very obvious, that the above sketch, even as a sketch, remains very incomplete. A general phytogeographical map of South Africa might be attempted on the lines indicated, but it could only be completed with anything approaching accuracy if those interested, who are resident in various parts of the sub-continent, were willing to cooperate.

As to the more obvious gaps in our knowledge a few of the more important may be set down. 1. An account of the Strand Association right round the coast. 2. The distribution of Fynbosch or Macchia outside the south-western region where it is the dominant type. 3. The interrelationships between Grass Veld and Karroo, with an account of the detailed succession in the latter. 4. The exact distribution of the different types of Tree Veld (Thorn Veld, *Protea* Veld, Bush Veld, etc.), and far more details regarding the controlling factors, both climatic and edaphic. 5. An account of the vegetation in salt or "brak" places in the dry interior. 6. An investigation

into the general ecological character and relationships of Succulent and Thorny Scrub. 7. An investigation into the question of how much of South Africa is to be classified as desert.

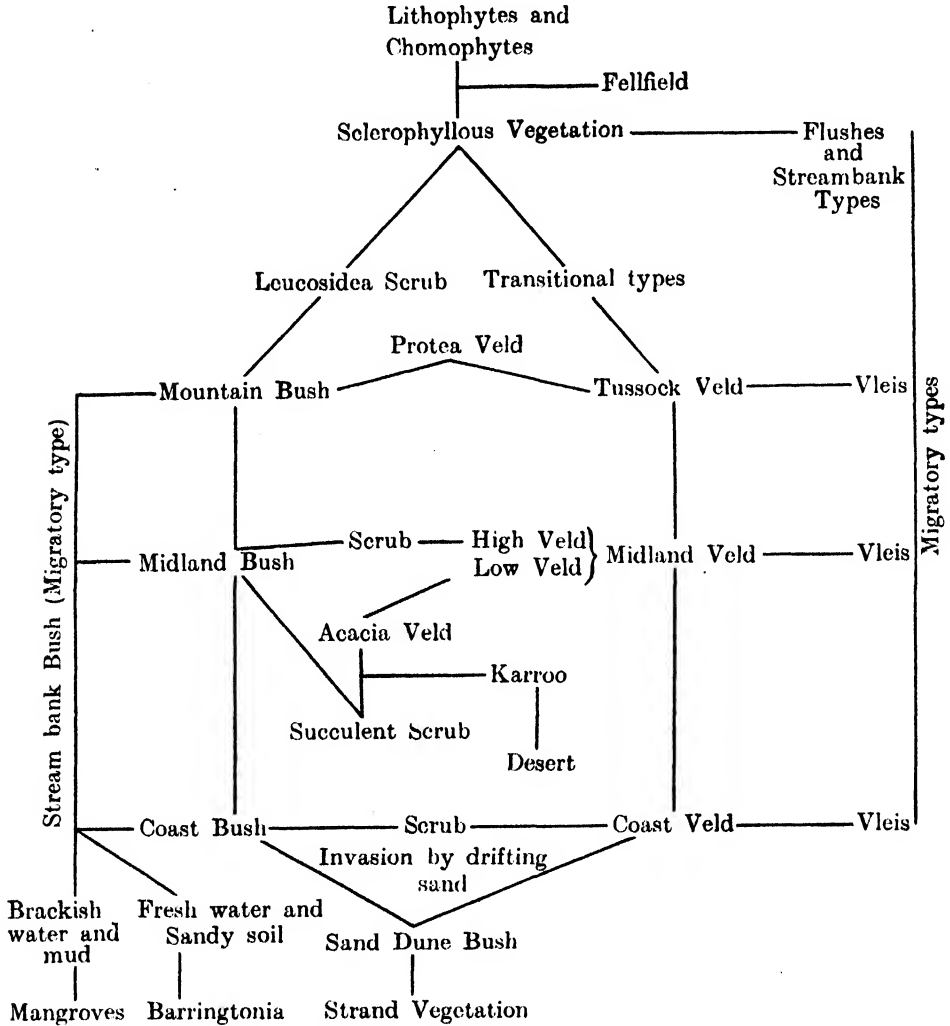


FIG. 19. Scheme showing relationships between the types of South African Vegetation described in the text.

Such contributions to our knowledge are necessary to enable us to complete a very general "primary survey" of the vegetation, without touching more intensive work, involving problems that are almost endless.

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OSMOTIC PRESSURE IN ROOTS AND IN LEAVES IN RELATION TO HABITAT MOISTURE

BY V. ILJIN, P. NAZAROVA AND M. OSTROVSKAJA

I. INTRODUCTION

Various investigators have demonstrated the importance of osmotic pressure as a factor regulating the passage of water from cell to cell and its absorption from the soil.

The fact that young leaves retain their freshness for a longer period of time than older ones has been explained by Pringsheim (10), for wilting succulents, as the result of the more intense osmotic pressure of younger leaves. Moreover he has found more concentrated cell-sap in developing buds than in reserve organs like bulbs and tubers which are able to produce shoots without any extraneous water supply. According to this author's view, not only the earlier wilting but also the complete drying of adult parts of plants may be explained by the comparatively low osmotic pressure in these parts.

But it is hardly possible to explain exclusively by reduced osmotic pressure the complete drying of plants; this phenomenon may be connected with some secondary factors invoked by the wilting, which leads to the death of tissues. The cells with low sap concentrations will really show earlier wilting, but at the same time further concentration will take place and therefore arrest the loss of water; further loss of water is possible only in the case of simultaneous death of young as well as old organs, which apparently does not take place.

Renner (11), who investigated the absorption of water by shoots, found that there may be developed within plants an absorbing power reaching 10-20 atmospheres of negative pressure. This power has been related by Nathanson (9) to the osmotic power of the leaf tissue, and he has shown that its intensity may be expressed by the difference of the osmotic pressure in the roots and in the leaves. Hannig (4) made a number of determinations for the roots and leaves of xerophytes, mesophytes, hygrophytes and floating and submerged hydrophytes and expected to find the greatest difference in the former and the smallest in the latter; but the results he obtained, as summarised in Table I, show that the percentage of species showing equality

of osmotic pressure in roots and leaves (upper line) is the same in all four groups, except hygrophytes, in which the percentage of species showing the greatest difference between roots and leaves, i.e. the ratio 1 : 2, is higher than in the other groups.

TABLE I

Relation of osmotic pressure in roots to that in leaves	Xerophytes (11 species)		Mesophytes (17 species)		Hygrophytes (15 species)		Floating and submerged plants (6 species)	
	No. of species	Per cent.	No. of species	Per cent.	No. of species	Per cent.	No. of species	Per cent.
1 : 1	2	18	3	18	1	7	1	17
1 : 1-1.25	5	45	10	59	6	40	4	66
1 : 1.25-1.50	1	10	2	17	2	13	1	17
1 : 1.50-2.00	3	27	2	17	6	40	0	0

Fitting (3), who studied desert plants, claims for osmotic pressure an important part in the process of water absorption from dry and salt (alkali) soils. On his view, the osmotic pressure may set up a reacting force to the adsorbing power of soil particles, and the more intense the reaction of the root cells the larger the amount of water they absorb. Fitting has given a number of measurements, using always the leaves and not the roots, as he assumed that the osmotic pressure in both organs is identical. The results of his experiments have shown a rather high osmotic pressure in plants growing in deserts, and regular oscillations have been observed which are to be connected with the percentage of moisture in the locality. The osmotic pressure in oases and on cultivated soils was weaker than on dry, stony desert soils; in the latter case it was even more intense than in plants growing on alkali soils. Keller (6) has observed a similar phenomenon in the plants of Russian deserts.

According to Fitting the high osmotic pressure of root cells is able to exercise an influence on the absorption of water adsorbed by soil, i.e. it can overcome the inter-cohesion of the soil particles. This cohesive power certainly plays a part in the phenomenon of adsorption, but in osmotic phenomena we have to deal with the diffusion of substances through the semi-permeable cell membranes in the direction of weaker concentration. In the case of water absorption by the root free water passes out of weak concentration in the soil into the cell, which possesses a more concentrated solution, hence we have to deal only with the diffusion of free (not colloiddally bound) substance. Briggs and Shantz (1), who studied the amount of water remaining in the soil after the wilting of plants, found that representatives of quite different ecological types left the same amount of unabsorbed (non-available) water behind in the soil after their wilting. These authors remark that the growth of the plants investigated took place in soils having different percentages of moisture. Soil moisture, as shown by Pringsheim (10) as well as by our own experiments, strikingly affects the intensity of osmotic pressure. Plants of *Cucurbita pepo*, sown under different conditions, have

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shown quite different osmotic pressures, as seen in Table II, compiled from Pringsheim's results.

TABLE II

Conditions of culture				Osmotic pressure in normal solution of KNO_3
(1)	Pot set in water; surrounding atmosphere wet	0.14-0.16
(2)	Pot set in water; air that of a forcing-house	0.18
(3)	Normal watering; air that of a forcing-house	0.24-0.26
(4)	Infrequent watering; the air that of a forcing-house	0.42-0.44
(5)	Absolutely dry; the air that of an ordinary room	0.55

Similar results have been obtained in our own experiments (Table III).

TABLE III

Names of plants	Ratio of soil moisture to absolute water- capacity of soil	Osmotic pressure in normal solution of NaCl
<i>Helianthus annuus</i>	{ 80 %	0.14-0.16
	{ 60 %	0.25-0.28
	{ 30 %	0.41-0.45
<i>Zea mays</i>	{ 80 %	0.17
	{ 60 %	0.19
	{ 30 %	0.49

Fitting's view that the intensity of the osmotic pressure may affect the amount of non-available water would therefore seem quite unfounded. Fitting himself refers to the results obtained by Livingston, who showed that in the shallow layers of the soil on the Arizona deserts, in which grow the roots of the plants investigated, there is a sufficient amount of water. According to Livingston's observations (7), made during the driest season, there was at the depth of 13-35 cm. as much as 13-16 per cent. of water, whilst the wilting of plants, even such as *Vicia faba* and *Phaseolus multiflorus*, grown on such soil took place only at 10-11.62 per cent. of moisture. Thus the growth of plants seemed to be secured even without special arrangements helping to absorb the water.

As to Fitting's numerical data, it is rather doubtful that they could characterise the real intensity of the osmotic pressure in the roots.

According to Dixon's measurements (2), the difference of the osmotic pressure in the roots and in the leaves may be very substantial. Thus, in the roots of *Eucalyptus* the pressure was equal to 5.3 atmospheres and in the leaves to 6-8 atmospheres. A still greater difference was found by this author in lilac—in the roots 4.3-5.9 atmospheres and in the leaves 11.6-26.9 atmospheres. Our observations gave even more striking results, as is to be seen from Table IV.

The numbers show that the relation of the pressure in leaves and in roots may be equal 1 or even be much higher; for instance in *Calamagrostis epigeios* it is 4.26 greater in the leaves. At any rate the osmotic pressure in the

epidermis of the leaves gives us no indication of the osmotic pressure in the roots.

TABLE IV

Names of plants	Osmotic pressure in normal solution of NaCl		
	Leaves	Roots	Ratio
<i>Veronica beccabunga</i>	0.15	0.15	1.00
<i>Alisma plantago</i>	0.15-0.20	0.15-0.20	1.00
<i>Centaurea sibirica</i>	0.65	0.55	1.18
<i>Calamagrostis epigeios</i>	0.64	0.15	4.26
<i>Lythrum virgatum</i>	1.15	0.28	4.11
<i>Typha latifolia</i>	0.80	0.20	4.00

II. METHODS USED

The intensity of the osmotic pressure is clearly of great importance since it may materially influence the rate of water absorption, and particularly under natural conditions of competition the usual struggle for existence. Two osmotic systems of different power, plunged into water or into wet soil, will obviously absorb at different rates—the system having the more concentrated solution of substances will be supplied with a larger amount of water per unit of time. Again, more concentrated solutions of substances in the cell will retard coagulation and death of plasma which take place when water is lacking in a very dry habitat; such protective action has been pointed out by Maximov (8) in investigating the freezing of plants, when the plant dies in consequence of the lack of water incurred by the presence of ice. It is then quite evident that the study of osmotic pressure is important in ecological investigations.

The investigations here recorded have been made by us on the reserved areas of the Prairie Biological Station of the Petrograd Imperial Society of Naturalists on the estate of the Countess Panina, situated in the Valujsky district, government of Voronezh.

The roots for investigation were taken at the depth of 30 cm., together with the surrounding soil which was then detached by a powerful jet of water. The osmotic pressure was determined by method of plasmolysis in the cortical parenchyma, in the parts covered with root hairs and therefore active with regard to water absorption.

In order to determine the osmotic pressure in the leaves, the epidermis was investigated. Now the question arises whether the latter can characterise the mesophyll, which is the actual water evaporating tissue. Comparative measurements were made in both tissues in the case of four species, and complete coincidence was obtained. Apart from this reference may be made to Iljin's work (5) on stomata, in which similar measurements were repeated many times and corresponding results obtained.

Three types of vegetation have been chosen for the investigation—

swamp, meadow and grass steppe—as being quite different with regard to their flora and the environmental conditions.

On the grass steppe *Festuca ovina* and *Stipa capillata* are dominant, usually accompanied by *Bromus erectus* and *Koeleria gracilis*; *Poa pratensis* and *Triticum repens* are abundant, while among the dicotyledonous plants there were observed *Garagana frutescens*, and on more bare places *Centaurea sibirica* as well as *Aster villosus*, *Artemisia austriaca*, etc.

The meadow bears a rather dense and high covering of grasses and dicotyledonous plants; the most typical were *Poa pratensis*, *Triticum repens*, *Phleum pratense*, *Alopecurus pratensis*, *Calamagrostis epigeios*, *Geranium pratense*, *Centaurea jacea*, *Galium rubioides*, *Lysimachia nummularia*, *Sanguisorba officinalis*, *Lychnis alba*, etc.

The plants growing on the edges of the swamp are *Alisma plantago*, *Veronica beccabunga*, *Lythrum virgatum*, *Polygonum hydropiper*, *Bidens cernuus*, etc., and in the water *Typha latifolia*.

Observations were made on the environmental conditions in these three habitats. In Table V are shown the results of soil moisture determinations

TABLE V

Depth from surface	August 3		August 8		August 13		August 19		August 30		September 7	
	Meadow	Steppe	Meadow	Steppe	Meadow	Steppe	Meadow	Steppe	Meadow	Steppe	Meadow	Steppe
			21.4	21.9	25.4	12.7		23.7	31.1	28.9	31.5	27.9
10 cm.	31.6	26.8	25.1	23.9	23.8	16.1	24.3	23.5	21.6	26.4	26.9	27.1
20 "	28.2	26.1	21.5	21.2	23.2	16.8	20.3	18.5	21.8	22.0	21.8	24.6
40 "	26.5	20.1	20.5	19.4	21.1	18.5	19.9		20.4	16.9	24.4	19.7
70 "	18.7	15.5	15.8	14.2	23.1	15.7	18.6	15.1	21.2	15.1	21.2	14.9
100 "	23.4	14.5	16.9	14.2					24.6	15.1		

in the meadow and the steppe during different periods. It may be remarked that the work at the Station could not be commenced until rather late in the year (end of July). As far as the swamp is concerned, its soil is always saturated with water. The moisture of the soil on the meadow was greater in all layers than that of the steppe. It was only in August, when the rains began, that a more considerable amount of moisture in the upper layers of the steppe became noticeable, these layers being more penetrable by precipitations in consequence of the less dense plant covering. The amount of available water and the conditions of water loss are clearly less favourable for the steppe plants than for those of the meadow and the swamp.

The conditions of evaporation have been determined with the aid of atmometers constructed according to Livingston's pattern (7). In Table VI the amount of evaporation on the meadow and on the steppe is shown, while Table VII gives the evaporation on the swamp, on the meadow and on the steppe. The evaporation proceeded the whole twenty-four hours and the countings were made at 8 a.m., 2 p.m. and 7 p.m.

Table VI shows that evaporation on the meadow during the night (7 p.m.

—8 a.m.) is rather weak in comparison to the steppe. On August 9–10 it was half as much, on July 31 and August 1 one-fifth, on July 26–27 one-sixth, and on August 15–16 one-seventeenth. During the day time it has been about half as much on the meadow as on the steppe, and on especially wet days (August 15–16, 8 a.m.–2 p.m.) only one-sixth.

TABLE VI

Dates	Hours of the day	Evaporation in c.c.	
		Meadow	Steppe
July 26–27	7 p.m.–8 a.m.	0.3	1.8
	8 a.m.–2 p.m.	4.1	7.7
	2 p.m.–7 p.m.	1.6	4.3
July 31–August 1	7 p.m.–8 a.m.	0.4	2.1
	8 a.m.–2 p.m.	5.1	9.6
	2 p.m.–7 p.m.	2.3	5.4
August 9–10	7 p.m.–8 a.m.	0.5	1.2
	8 a.m.–2 p.m.	4.6	6.4
	2 p.m.–7 p.m.	1.2	2.2
August 15–16	7 p.m.–8 a.m.	0.1	1.7
	8 a.m.–2 p.m.	0.3	1.8
	2 p.m.–7 p.m.	1.9	3.7

TABLE VII

Dates	Hours of the day	Evaporation in c.c.		
		Swamp	Meadow	Steppe
August 20–21	7 p.m.–8 a.m.	0.3	2.2	5.5
	8 a.m.–2 p.m.	1.7	3.9	5.1
	2 p.m.–7 p.m.	0.3	1.3	2.0
August 24–25	7 p.m.–8 a.m.	0.1	0.9	2.5
	8 a.m.–2 p.m.	2.3	6.0	7.5
	2 p.m.–7 p.m.	1.6	2.1	2.7
August 29–30	7 p.m.–8 a.m.	0.2	0.4	0.6
	8 a.m.–2 p.m.	1.2	3.3	4.7
	2 p.m.–7 p.m.	1.3	2.4	3.4
September 3–4	7 p.m.–10 a.m.	0.3	1.5	3.1
	10 a.m.–3 p.m.	0.4	1.2	2.0
	3 p.m.–8 p.m.	0.3	1.1	1.6

Table VII shows us that evaporation on the swamp has been even lower than that on the meadow.

III. OSMOTIC PRESSURE IN RELATION TO HABITAT

Let us see first how the osmotic pressure in the roots of plants growing in different habitats is distributed.

The methods being rather complicated, the measurements have not proceeded simultaneously in all the habitats and in all the plants. They were made during the following periods: steppe plants July 25–28, meadow plants July 29 to August 1, swamp plants after August 9. One may presume that no striking changes would be found in the latter because they had been all the time saturated with water.

Control experiments have been made throughout, in order to ensure that no occasional results have been registered and that the period of 2–3 days

could not produce any change in the measurements. Two parallel observations have mostly been done, and in some cases even three and four; the results obtained were always identical.

The results are summed up in Table VIII. The numbers joined by dashes show that the number is between these two limits and has not been exactly determined.

The highest osmotic pressure is shown by the steppe plants, this being approximately equal to 0.40–0.48 of normal solution of NaCl. The meadow plants have osmotic pressure equal to 0.19–0.30 and the swamp plants only 0.13–0.20. Hence the roots of steppe plants should possess greater water absorbing capacity and greater drought resistance.

TABLE VIII

Dates	Names of plants	Osmotic pressure in normal solution of NaCl
Steppe		
July 25	<i>Triticum repens</i>	0.40
„ 28	<i>Bromus erectus</i>	0.41
„ 28	<i>Festuca ovina</i>	0.40–0.45
„ 27	<i>Koeleria gracilis</i>	0.45
„ 27	<i>Caragana frutescens</i>	0.45
Meadow		
„ 29	<i>Calamagrostis epigeios</i>	0.15–0.19
„ 29	<i>Triticum repens</i>	0.30
August 1	<i>Galium rubioides</i>	0.23–0.30
„ 1	<i>Lysimachia nummularia</i>	0.23–0.30
„ 1	<i>Lythrum virgatum</i>	0.23–0.30
Swamp		
„ 9	<i>Veronica beccabunga</i>	0.15
„ 10	<i>Alisma plantago</i>	0.15–0.20
„ 27	<i>Lythrum virgatum</i>	0.12
September 13	<i>Lythrum virgatum</i>	0.18
„ 14	<i>Typha latifolia</i>	0.20

It is quite natural to presume that the energy of osmotic pressure here depends upon the soil moisture. If consequently there be modifications in the latter, the former will change too. Alteration in the soil moisture may depend either upon the situation or upon the climatic conditions during the vegetative period. It is therefore presumable that in the habitat possessing a great deal of moisture the osmotic pressure of a given species will be lower than that of the same species growing in a drier locality; the same consideration is applicable to the climatic periods.

We may consider first the moisture conditions, and shall enquire how the external conditions of the habitat affect the intensity of osmotic pressure.

From Table V, given above, we can see that moisture of the soil on the meadow is greater than on the steppe. The meadow steppe is the intermediate type between these two habitats.

In Table IX is shown the distribution of the moisture in the soil in these three habitats. In Table X are shown the amounts of evaporation from atmometers.

TABLE IX

Depths from surface	Meadow	Meadow steppe	Grass steppe
	25.35	18.56	12.73
10 cm	23.75	19.18	16.07
20 "	23.19	19.43	16.84
40 "	21.12	18.97	16.47
70 "	23.07	18.15	15.68

TABLE X

Dates	Hours of the day	Evaporation in c.c.		
		Meadow	Meadow steppe	Grass steppe
July 31-August 1	7 p.m.-8 a.m.	0.4	0.8	2.1
	8 a.m.-2 p.m.	5.1	8.4	9.6
	2 p.m.-7 p.m.	2.3	5.1	5.4
August 9-10	7 p.m.-8 a.m.	0.5	0.7	1.2
	8 a.m.-2 p.m.	4.6	5.1	6.4
	2 p.m.-7 p.m.	1.2	1.9	2.2
August 15-16	7 p.m.-8 a.m.	0.1	0.2	1.7
	8 a.m.-2 p.m.	1.9	3.6	3.7
	2 p.m.-7 p.m.	2.3	5.4	7.2

Together with the changes in the percentage of the moisture in the environment the osmotic pressure of the same species varies too, as is shown in Table XI. *Poa pratensis* on the meadow steppe has pressure equal to

TABLE XI

Date	Names of plants	Habitat	Osmotic pressure in normal NaCl
August 13	{ <i>Poa pratensis</i>	{ Steppe	0.40-0.45
" 15		{ Meadow	0.37
" 16	{ <i>Triticum repens</i>	{ Steppe	0.38-0.41
" 17		{ Meadow	0.35
" 24	{ <i>Festuca ovina</i>	{ Steppe	0.30
" 26		{ Hollow	0.23
" 29	{ <i>Koeleria gracilis</i>	{ Grass steppe	0.28-0.30
September 1		{ Meadow steppe	0.20
August 27	{ <i>Stipa capillata</i>	{ Grass steppe	0.40-0.42
August 27		{ Meadow steppe	0.30
September 12	{ <i>Lythrum virgatum</i>	{ Dry swamp	0.28
August 18		{ Meadow	0.20
" 18		{ Shore of lake	0.20
September 13		{ " "	0.18
August 24		{ Lake	0.12

0.40-0.45 of normal NaCl, whilst on the meadow it has pressure 0.37. The same is to be observed in *Triticum repens*. *Festuca ovina* on the grass steppe has pressure equal to 0.30 and in the wet hollow 0.23. *Koeleria gracilis* on the grass steppe has pressure equal to 0.28-0.30, on the meadow steppe only 0.20. *Stipa capillata* shows on the grass steppe 0.40-0.42, and on the meadow steppe 0.30.

Special attention was attracted to *Lythrum virgatum*. The roots of this plant where deeply sunk in wet mud showed exceptionally low osmotic pressure, which was equal to 0.12 of the normal NaCl. On the shore of a forest lake, on soil quite wet but not saturated with water, among a thick growth of *Carex*, it reached 0.18 of normal NaCl. On the shore of a steppe lake, where the soil was bare, the pressure reached 0.20, as on the meadow. On dry swamp, with porous soil, which easily becomes dry during the hot season, the pressure reached 0.28 of normal NaCl.

Now we will examine how the osmotic pressure in the roots of the same species in the same habitat is affected by the changes of climatic conditions during the vegetative period.

The best climatic conditions were observed at the end of July and the beginning of September.

The meteorological data obtained (Table XII) show that from the beginning of August the atmospheric phenomena favour the appearance of a greater amount of moisture. The temperatures decrease—those of different hours of the day and the daily mean temperature, as well as maximal and minimal temperatures. The moisture of the air and cloudiness increase, the latter especially in the morning. The number of sunny hours in the day diminish. The amount of precipitation is not shown in the Table, because the absolute amount may not always characterise the extent of the moisture of the period in question. More important would be data with reference to the duration of precipitations, which may strikingly affect the moisture of the soil as well as that of the air and may therefore modify the water supply of plants. Not only will a more marked watering of the soil take place, but also the moisture of the air will considerably change.

TABLE XII

Periods of observation	Temperature						Moisture			Cloudiness			Hours of sunshine per day
	7 a.m.	1 p.m.	9 p.m.	mean	maximal	minimal	7 a.m.	1 p.m.	9 p.m.	7 a.m.	1 p.m.	9 p.m.	
July 23–August 2	18.8	26.0	16.0	20.3	28.4	12.0	76	52	74	3.9	5.3	4.5	8.4
August 3–13	16.2	22.6	15.4	20.1	25.4	13.2	83	59	82	4.4	6.3	4.1	7.7
August 14–23	12.9	19.9	15.1	15.9	20.8	8.9	82	55	76	5.7	7.7	6.2	5.3
Aug. 11–Sept. 2	11.9	17.0	12.1	13.6	18.9	8.5	83	65	84	7.1	7.0	4.2	5.1
September 3–7	8.3	13.4	8.9	10.2	12.3	5.0	93	69	87	7.6	8.2	5.4	2.6

An interesting example of this kind may be provided by the following. In the meteorological bulletin it is indicated that on August 5 there fell during one hour 67.0 mm. of precipitations, whilst during eleven days (August 26–September 6) there fell only 28.6 mm. The latter period is, however, in reality the wetter, for during these eleven days there were three days absolutely dry, whilst on other days there were almost incessant rains. The heavy rain which took place on August 5 did not produce much impression

on the soil moisture; on August 6 the latter was about the same as on August 3. Enormous water currents ran away along the soil declivities without having touched the deeper layers of the soil. On the other hand the later rains greatly affected the soil moisture, as is shown in Table V. They had a special influence upon the grass steppe, which had low and distantly growing grasses. The upper layers of this prairie were in the beginning of September much moister than those of the meadow.

According to climatic changes, the osmotic pressure in the roots had considerably changed, as is to be seen from Table XIII, where the intensity

TABLE XIII

Names of plants	Dates	Osmotic pressure in normal solution of NaCl
<i>Festuca ovina</i>	{ July 28	0.40-0.45
	{ August 26	0.30
<i>Koeleria gracilis</i>	{ July 27	0.45
	{ August 29	0.28-0.30
<i>Bromus erectus</i>	{ July 28	0.41
	{ September 8	0.15-0.20

of osmotic pressures of the plants growing on the grass steppe at the end of July and at the end of August is shown. The latter period shows a marked decrease in comparison with the former, especially in *Bromus erectus*, the measurements of which were made in the beginning of September when the soil of the grass steppe was much better watered than that of the meadow.

IV.

We now turn to the osmotic pressure in the leaves, and devote our attention to the question how the osmotic pressure is distributed in plants growing in different habitats, and what relation is to be observed between roots and leaves.

In Table XIV are shown the results of measurements made on the leaves and the roots of plants growing in different situations.

These numbers show that the osmotic pressure in the leaves gives us no criterion to judge this in the roots. The relation of the pressures in these two organs may show noticeable changes, as indicated in the right-hand column of Table XIV.

Fitting, as mentioned above, declares that the osmotic pressure in the leaves of plants growing in dry places will be higher than that of plants growing in wet and moist localities. Our results show, however, that the absolute osmotic pressure in the leaves of the swamp plants is higher than in those of other plants; though that in the roots is lower in swamp than in meadow plants, and in the roots of meadow plants it is less than in those of steppe plants.

TABLE XIV

Date	Names of plants	Osmotic pressure in normal solution of NaCl		
		Leaf	Root	Ratio
Steppe				
July 28	{ Bromus erectus }	0.72		1.77
„ 30			0.41	
„ 28	{ Festuca ovina }	0.60-0.75		1.59
„ 31			0.40-0.45	
August 10	Centaurea sibirica	0.65	0.55	1.18
„ 14	Poa pratensis	0.50	0.40-0.45	1.18
Meadow				
July 29	{ Calamagrostis epigeios }	0.60-0.75		3.97
August 1			0.15-0.19	
„ 1	Lythrum virgatum	0.70-0.75	0.20-0.30	2.90
July 29	{ Triticum repens }	0.75-0.90		2.75
August 1			0.30	
„ 1	Galium rubioides	0.30	0.23-0.30	1.13
„ 1	Lysimachia nummularia	0.30	0.23-0.30	1.13
„ 14	Poa pratensis	0.37	0.37	1.00
Swamp				
„ 12	Lythrum virgatum	0.85	0.18	4.70
„ 13	Typha latifolia	0.80	0.20	4.00
„ 5	Veronica beccabunga	0.15	0.15	1.00
„ 5	Alisma plantago	0.15-0.20	0.15-0.20	1.00

According to Hannig's hypothesis the biological groups differ one from another by the difference of the pressure in the roots and in the leaves, which creates a sucking power. This power should be greatest in steppe plants and lowest in swamp plants. We can, however, see that in reality there are representatives of all groups having the same or almost the same osmotic pressure in the roots and in the leaves, and there are also representatives which have quite different intensities of osmotic pressure in these two organs.

All these correlations may be explained from another point of view. The intensity of osmotic pressure, as stated above, may materially influence the process of water absorption by the cells. The cells having more concentrated solutions will more energetically absorb the water, the conditions of water supply being the same. Leaves which are under conditions of more intense evaporation, as are the upper leaves of a plant, require more energy for absorbing water than will the lower leaves which do not project beyond the surrounding grasses or other competing vegetation. Moreover, the upper leaves will surely stand in greater need of the protecting effect of dissolved substances which impede the coagulation of the plasma.

If however we put aside such a teleological point of view and assume that the intensity of osmotic pressure is merely a function of the moisture of the environment, we must expect to find higher pressure in the upper leaves, which stand above the surrounding grasses, etc., and can be reached by dry and moving air.

Table XIV shows that low osmotic pressure in leaves, identical with that of roots, may be found in leaves deeply plunged into the thickly growing

surrounding grasses or in those leaves which are always saturated with water vapour, for instance in *Veronica beccabunga*, young shoots of *Alisma plantago*, *Lysimachia nummularia*, *Galium rubioides*, *Poa pratensis* and *Centaurea sibirica*. The two latter plants give leaf numbers which are, absolutely as well as with regard to the roots, greater than those for the other plants. This may be due to the fact that the grasses on the steppe do not grow so densely, hence the air is not so wet and the osmotic pressure in the roots is comparatively high. As to the other plants, the leaves of which were in free touch with the moving air, whether on account of the high stems or the distances between the grasses, the osmotic pressure in the leaves in these cases was (1) higher than in the roots, and (2) about equal in all the plants, being on the average equal to 0.70–0.80 of normal NaCl.

Hence we arrive at the same conclusion as that reached with reference to the roots, namely that the intensity of osmotic pressure depends upon the moisture in the environment. If we consider, therefore, leaves of the same kind (upper leaves or lower leaves), we find that their pressure will vary according to (1) the situations where the plants grow or (2) the climatic conditions. The osmotic pressure will be greater either in a drier situation or during a drier season.

Table XV shows the intensity of the osmotic pressure in the same species (1) during different periods of vegetation, and (2) during the same period but in different situations.

TABLE XV

Names of plants	Situation	Dates	Osmotic pressure in
			normal solution of NaCl
Bromus erectus	{ Grass steppe	July 30	0.72
	{ " "	September 8	0.50
	{ Meadow steppe	" 5	0.40
Koeleria gracilis	{ Grass steppe	July 31	0.60–0.68
	{ " "	August 29	0.56
	{ Meadow steppe	September 1	0.38
Festuca ovina	{ Grass steppe	July 31	0.60–0.68
	{ " "	August 26	0.45
	{ " "	" 24	0.30

Tables IX and X have shown us that the meadow steppe has a greater amount of moisture than the grass steppe, and the meteorological data show that the end of July was drier than the beginning of September. In accordance with these data, all three species growing on the grass steppe have shown in the latter end of July and in the first half of August a higher osmotic pressure than in the end of August and in the beginning of September, and in the latter period the pressure was higher in plants on the grass steppe than in those on the meadow steppe.

If we take into consideration the different kinds of leaves (for instance, upper and lower leaves) of the same individual, the osmotic pressure will be identical in both if they are under similar conditions, but not if the lower

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leaves are plunged among the thickly growing grasses and the upper leaves surpass the height of the surrounding grasses. This is shown by the results set forth in Table XVI. The plants growing in open places, where all the

TABLE XVI

Names of plants	Lower leaves placed	Osmotic pressure in the leaves in normal solution of NaCl		
		Upper	Lower	Relation
Peucedanum absaticum	Among grasses	0.56	0.52	1.08
Senecio doria	{ In open	0.50	0.43	1.16
	{ Among grasses	0.30	0.30	1.00
Centaurea scabiosa	{ Among grasses	0.56	0.41	1.37
	{ In open	0.56	0.56	1.00
Sanguisorba officinalis	{ Among grasses	0.60	0.39	1.54
	{ In open	0.53	0.53	1.00
Lythrum virgatum	Among grasses	1.12	0.53	2.11

leaves are under similar conditions, have the same osmotic pressure in upper and in lower leaves. If the latter are plunged into the thickly growing surrounding grasses the relation is modified, and the deeper the plunging is, the more striking becomes the difference.

If we apply the relation between the conditions of water supply and the intensity of the osmotic pressure in greater detail, we may conclude that the different parts of the same leaf will have unequal osmotic pressure, being under different external conditions. Thus a large leaf is differently susceptible in its different parts to the influence of the environment. A good example is provided by *Typha latifolia*, which has been taken for experiment. The lower part of the leaf was plunged into the water, its middle part was plunged in the thickness of the surrounding grasses and its top stood open above the grasses. As is shown in Table XVII, a continuous increase in the osmotic pressure is observed in going from the bottom up to the top.

Apart from external influences, the construction of the leaf itself may affect the water supply. The edges and the middle, the top and the

TABLE XVII

Part of the leaf (<i>Typha latifolia</i>)	Osmotic pressure in normal solution of NaCl
Under the water	0.23
10 cm higher than the level of water	0.30
125 " " "	0.64
250 " " "	0.80

bottom will consume different amounts of water and will be, therefore, under different conditions as to water supply. Measurements of osmotic pressure were made in different parts of the leaf, near the main nerve, as well as near the edge. In all cases the measurements were made on leaves having parallel lateral veins. The results are summarised in Table XVIII, where are shown the dimensions of the leaf, as well as the osmotic pressure on the edge and near the lateral vein. The measurements of *Saxifraga cordata*, *Arabis alpina*,

TABLE XVIII

Names of plants	Dimensions of the leaf		Osmotic pressure in normal solution of NaCl		
	Width	Length	Edge	Middle	Relation
<i>Verbascum lychnitis</i>	13	39	0.64	0.43	1.49
<i>Saxifraga cordata</i>	12	29	0.58	0.46	1.26
<i>Senecio doria</i>	13	34	0.48	0.46	1.04
<i>Verbascum lychnitis</i>	6	14	0.43	0.40	1.08
<i>Arabis alpina</i>	4	9.2	0.59	0.54	1.09
<i>Rumex acetosa</i>	4	11	0.29	0.29	1.00
<i>Centaurea scabiosa</i>	4	13	0.38	0.38	1.00
<i>Dianthus caryophyllus</i>	0.5	18	0.56	0.56	1.00
<i>Saxifraga aizoon</i>	0.5	4.2	0.62	0.62	1.00

Dianthus caryophyllus and *Saxifraga aizoon* were made in September in the Botanical Gardens of the University of Petrograd with cane sugar and not with NaCl. The larger leaves show a more sensible difference. A leaf of *Verbascum lychnitis* 13×39 cm. had the relation of the osmotic pressure near the edge to that in the middle equal almost to 1.5. A small leaf of the same plant gave a ratio of 1.08. In general, the wider the leaf the larger is this ratio.

Thus in the leaf, as well as in the root there is to be observed the influence of differences in water supply. The osmotic pressure varies under the action of external influences, as well as under that of internal structure. There is always observed a close relation between the intensity of osmotic pressure and the amount of water at the disposal of the plant cell.

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March, 1916.

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ON THE VEGETATION OF FOUR DURHAM COAL-MEASURE FELLS

I. GENERAL DESCRIPTION OF THE AREA AND ITS VEGETATION

By HAROLD JEFFREYS

(With Plate XI and three Figures in the Text)

INTRODUCTION

The term "fell" is extensively used in the North of England to denote a tract of elevated country in a more or less uncultivated condition. Well-known examples are Scafell, Cross Fell, Bow Fell and Widdybank Fell. In the west of Durham, where the underlying rocks are mainly the coarse sandstones of the Bernician and Millstone Grit series, the ground on them is mostly covered with thick peat, and the principal dominant plants are *Calluna vulgaris*, *Eriophorum vaginatum*, and *Sphagnum* spp. (mainly *S. cymbifolium*)¹. The vegetation therefore belongs to the moor formation. In the east of the county, however, the coal measures outcrop, and many changes in the environment are associated with the geological change. The rainfall diminishes, the soils are mostly sand (often very fine) and clay, and the elevation is lower. Most of the west of the county is over 1000 feet in height, while in the coal measure area a hill of over 800 feet is a rarity. Peat is seldom or never formed, save in exceptional circumstances, and on some of the steeper slopes even humus is not to be found. The native vegetation is divided mainly between the heath, marsh, and neutral grassland formations, although the last is largely due to human interference, which is in most localities of considerable importance. The soil of N.E. Durham is readily cultivated, and the arable area considerably exceeds that under pasture. Natural woodland is nearly absent, and plantations usually line the steep banks of streams, as these are almost impossible to utilise otherwise.

The area (Fig. 20) is drained by the Rivers Tyne and Wear, and their tributaries. The only affluent of the Tyne that we need consider is the Team, a dirty stream about 13 miles in length, which rises near Annfield Plain,

¹ Lewis, F. J., "Geographical distribution of vegetation in the basins of the Eden, Tees, Wear and Tyne." *Geogr. Journ.* **28**, 1904, pp. 313-331.

flows east for 8 miles, and turns northwards at Birtley, falling into the Tyne near Gateshead. From Birtley to Gateshead it follows the old valley of the Wear, known as the "Great Durham Wash." Of the tributaries of the Wear, the most important for our purpose are the Cong Burn and the South Burn, which enter the main stream respectively at the north end of Chester-le-Street and a mile south of that town.

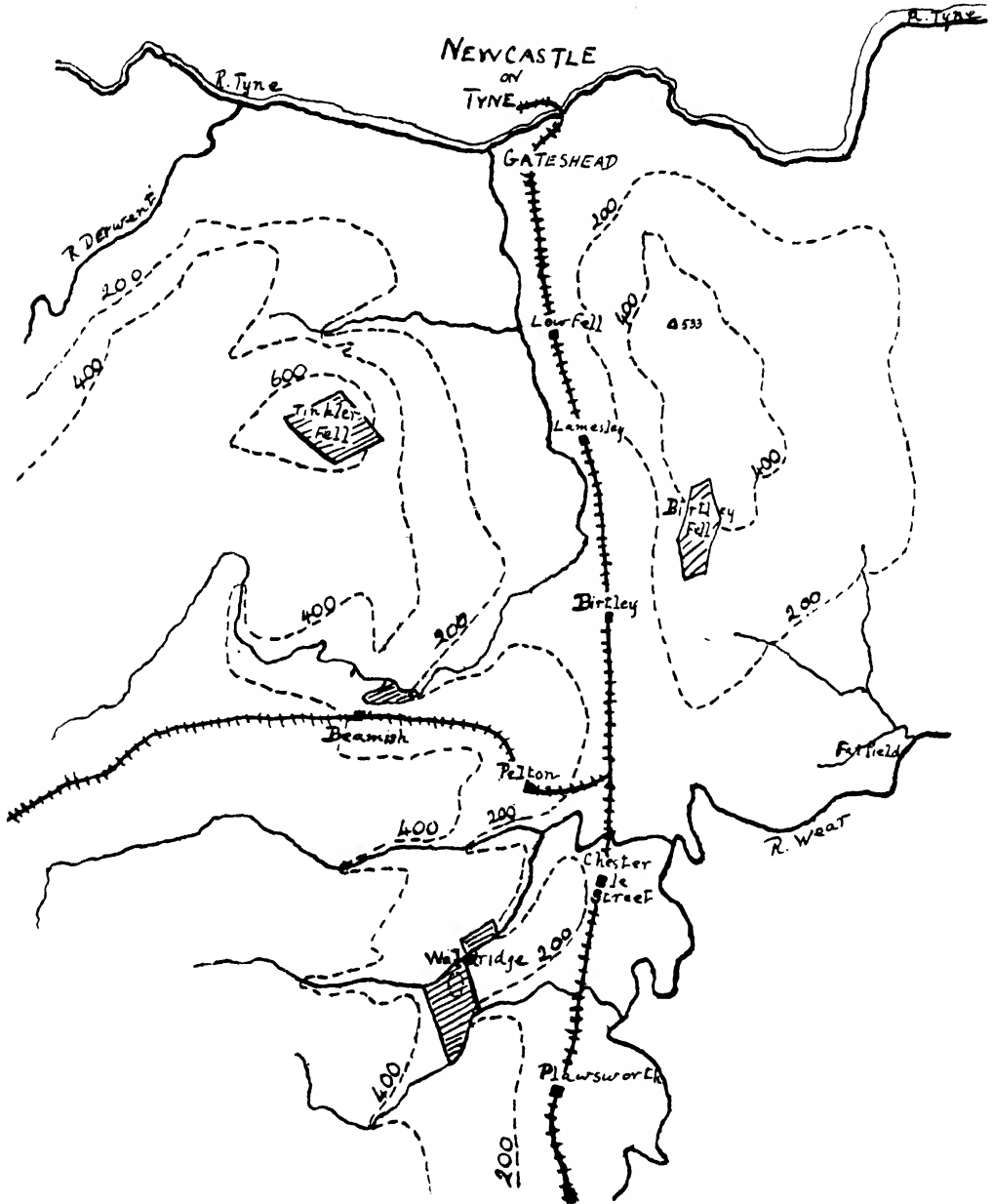


FIG. 20. Map showing the position of the areas dealt with.
Scale: 1 inch to 2 miles (1:126,720).

The Team flows in a wide and low valley, and on the sides of it rise the steep Ravensworth Hills and the Sheriff Hill range. The ground remains low between Birtley and Chester-le-Street; to the south-west of this is the elevated ground of the Waldrige and Edmondsley neighbourhood. Geologically this is probably continuous with the Ravensworth Hills.

The four fells to be described in this paper are Waldrige Fell, Beamish Fell, Birtley Fell, and Tinkler Fell.

The annual rainfall in the district is usually about 28 inches, but its seasonal distribution is very variable.

No British vegetation seems to have been described that bears any close resemblance to that of this area. That of the Pennines is widely different, and the moors of North-East Yorkshire¹, although on Jurassic rocks, resemble the Pennine moors more than the coal-measure heaths. The heaths of the New Forest are related to it, and some features of the coal-measure heaths show an affinity with the sandy areas of the Breck Country².

The present paper consists of a descriptive account of the vegetation; it is proposed to deal subsequently with experimental work that has been carried out on certain points connected with it. The maps have been taken from the 6-inch ordnance survey charts, and the details filled in from a triangulation. The general map of the district (Fig. 20) is derived from the half-inch Bartholomew map, sheet 2.

GENERAL DESCRIPTION OF THE FELLS CONSIDERED

Waldrige Fell, where most of the work in this paper has been done, lies about two and a half miles south-west of Chester-le-Street, and is a roughly rectangular area approximately half a square mile in extent. To the north of the village is a further tract of waste ground, disconnected from the main Fell but ecologically a part of it. The Fell is extremely irregular in its vertical section, ranging in height from 427 feet to 150 feet, while the hills are thirteen in number. The south-east side of the Fell is bounded principally by the South Burn, and the north-west side by the Cong Burn. These are both small streams, of a yellow colour owing to the oxidation of ferrous sulphate in the water, this being itself an oxidation product of the iron pyrites in the coal of neighbouring pits. The sides of these streams away from the Fell are mostly covered with plantations, excepting the portion of the South Burn to the south of the Chester Moor road. Here the Fell extends east of the stream to the top of a steep hill covered with bracken, while the moister ground in the valley is spontaneous and apparently natural woodland, of *Betula alba* on the right bank and *Alnus rotundifolia*

¹ Higge, F., "Eastern moorlands of Yorkshire." This JOURNAL, 2, 1914, p. 1.

² Farrow, E. P., "On the ecology of the vegetation of Breckland." This JOURNAL, 3, 1915, p. 211.

on the left. The right bank of the Cong Burn is an almost precipitous slope all the way, and from the point where the stream enters the Fell to the railway bridge it is covered with an oak-hazel wood. A sparse alder wood lines both banks of the stream much lower down, just before it leaves the Fell.

Many small streams rise within the area. The whole of the south-west side is drained by that marked 1 in Fig. 21, although this itself leaves the Fell immediately after its source in Bog 7. Stream 2 is a tributary of it, while those marked 3 and 4 end blindly in a depression containing numerous small *Juncus effusus* bogs. Streams 5, 6 and 7 are fed by the large Wanister bog (Bog 11), while 8, 9 and 10 also fall into the South Burn. A few small intermittent streams enter the Cong. Of all the fourteen streams in Fig. 21, however, only Nos. 1, 5 and 10 are permanent. The others all become dry in August. Most of the bogs also are not permanently wet, the exceptions being Nos. 4, 7 and 11. In addition the duck pond 5 never becomes dry, and Bog 13 very rarely does so. Both of these drain into the Wanister bog, though by no very definite channel.

Of the hills within the area, the highest is Hill 10, overlooking the village. The most striking in appearance, however, is the Wanister hill (Hill 2), on account of its sharp rise from the low-lying ground where the Wanister bog lies. Hills 6 and 7 are mere rubbish heaps, 8 is an old air shaft, and 11 is a pit heap. A bare and precipitous slope overhangs the valley that contains Bog. 7.

The general topography consists of a gradual but irregular rise from the South Burn and Stream 1 up to the ridge where Hills 10 and 12 stand. Round these is a plateau, with a steep slope to the north. The detached portion is likewise a plateau, sloping very rapidly to the Cong Burn, whose valley is indeed a ravine. A further interesting area is a disused pasture north-east of this, between the plantation and the burn. Pasturing is not extensive on the Fell, only a few ponies being fed, while rabbits occur only on Hills 1 and 3, and in the pasture just mentioned. On these two hills they are scarce, and apparently have little effect on the vegetation. They may have been more plentiful formerly, as the steep slope opposite Hill 13 is known as "Rabbit Banks."

The sandy areas are a large tongue extending from Hill 3 nearly to the rows of houses surrounding Pond 5, a smaller patch near the east corner, and the detached part. The rest is mainly clay, with varying quantities of sand.

Human interference is in evidence in several ways. Two waggon-ways intersect the Fell, but their effect on the vegetation seems very local. The heaps of shale from the collieries have a highly characteristic vegetation, as have also the Smithydene quarries near the Edmondsley road. The most interesting effects due to human agency are, however, the construction of footpaths and burning. The former appears to introduce two ecological

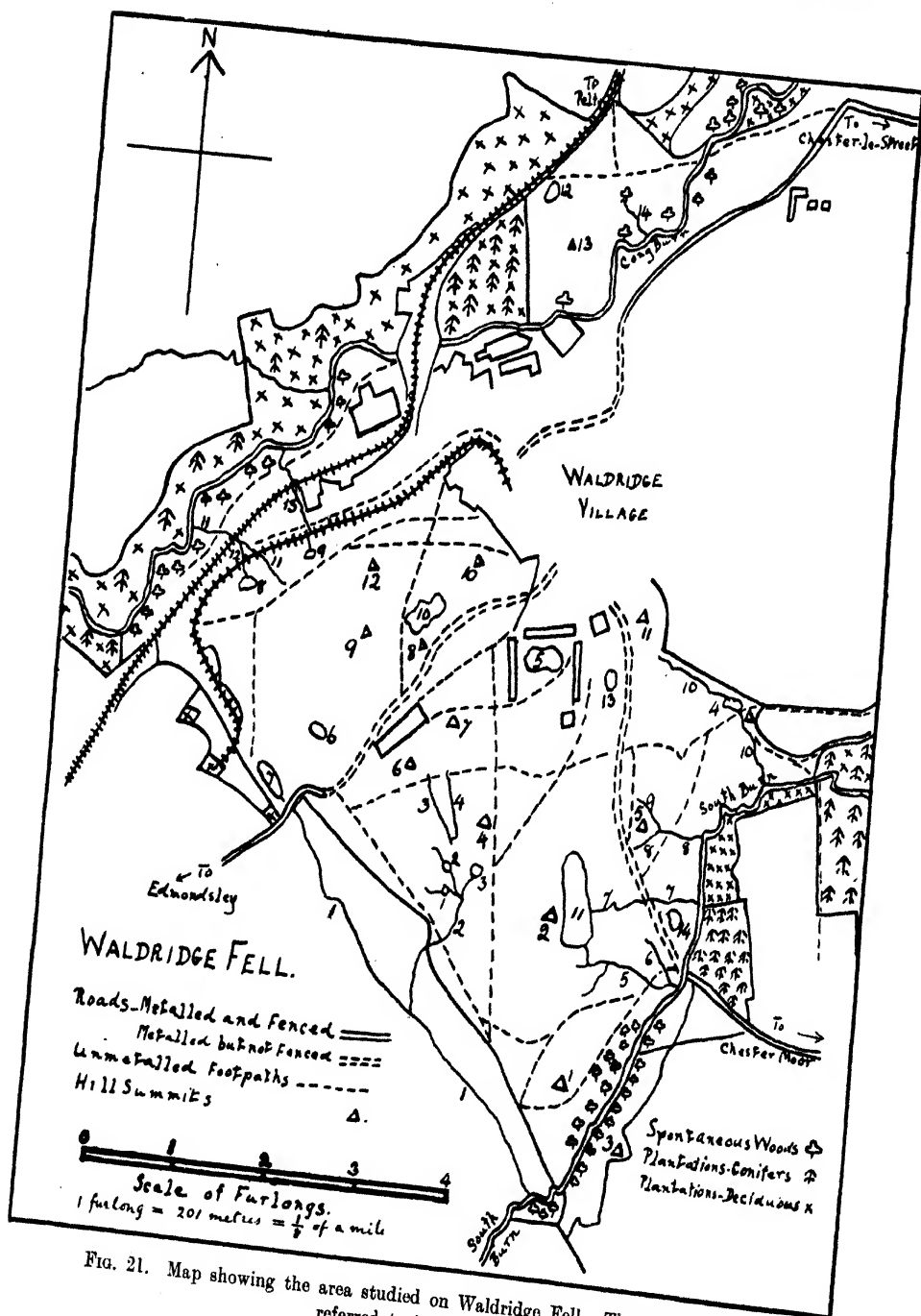


FIG. 21. Map showing the area studied on Waldrige Fell. The numbers are referred to in the text.

factors, namely, mechanical wear and water content. All of these effects on the environment must be regarded as in a sense biotic, although indirect in some cases. I have no evidence that any part of the Fell has ever been cultivated.

The following plants attain dominance on various parts of Walldridge Fell. Dry grassland:—*Festuca rubra*, *Agrostis vulgaris*. Heath:—*Pteris aquilina*, *Calluna vulgaris* (with *Empetrum nigrum*), *Vaccinium myrtillus*, *Ulex europaeus*, *Deschampsia flexuosa*, *Holcus mollis*, *Nardus stricta*. Intermediate:—*Holcus lanatus*, *Molinia coerulea*, *Carex goodenowii*. Marsh:—*Juncus glaucus*, *J. effusus*, *J. acutiflorus*, *Epilobium hirsutum*, *Glyceria fluitans*, *Sparganium ramosum*, *Eleocharis palustris*, *Alopecurus geniculatus*, *Agrostis alba*. Woodland:—*Quercus sessiliflora*, *Corylus avellana*, *Alnus rotundifolia*, *Crataegus monogyna*, *Betula alba*, *Salix cinerea*. Ruderal or transient:—*Senecio viscosus*, *Poa annua*, *Rumex acetosella*.

Beamish Fell is at the most southerly point of the course of the Team, which flows round three sides of it. The Team at this point is a pebbly stream about four yards across. The Fell rises steeply from it on all sides. Although not at present interfered with by man, it has probably been a plantation in quite recent times, as young trees of the Great Maple (*Acer pseudoplatanus*) occur frequently, and this tree is not indigenous. The area is marked as a plantation in the Ordnance Survey Map of 1850 under the name of Ousbrough Wood. The southern slope is indeed a young plantation now, and the whole area is marked as woodland in Bartholomew's map (sheet 2). To the north is an older plantation, mainly of Great Maple and *Quercus sessiliflora*. There is little variety in the vegetation, the only dominants being *Pteris aquilina*, *Deschampsia flexuosa*, *Holcus mollis*, *Betula alba*. The soil is very sandy, except on parts of the southern slope, where it is clay. There is no pasturage, and at present little human interference. Rabbits occur, especially near the top.

Birtley Fell lies about a mile and a half north-east of the town of Birtley, and is the southern extremity of the Sheriff Hill ridge. It is a long and narrow strip of elevated ground, running roughly north and south. In contour it is comparatively regular, being merely a fairly steady slope up to the most northerly point, where Shadon's Hill (487 feet) stands. There are no natural streams, but several ditches have been cut for drainage, apparently to adapt the area for pasture. Much of it is now enclosed and cultivated, but of the part that remains common land little has ever been ploughed. Three air-shafts disfigure the Fell, and there are only three ponds, all artificial and quite uninteresting duckponds. Two considerable bogs exist. A feature that has not, I believe, been explained, and that does not occur on any of the other fells, is the occurrence of many meres near the highest point. These are small depressions, varying in size. The largest are about three yards across and a yard deep, while the smaller are only

about one-third the size each way. Some are permanently filled with water, but most dry up in summer. The sides are very steep, and the water is peaty. They are probably to be attributed to very old pitfalls. The subsoil is stiff boulder-clay in the north and coarse sand in the south.

The area is much used for horse pasture, but rabbits are absent. There are few footpaths, but the Fell is used as a golf course, and much turfing takes place in order to repair the greens, and one long slope is regularly rolled. A first-class road runs along the east side, and a branch of it crosses the Fell, but is fenced. Burning occurs, but is not so extensive as at Waldrige.

Associations dominated by the following plants occur on Birtley Fell: *Agrostis vulgaris*, *Calluna vulgaris*, *Ulex europaeus*, *Nardus stricta*, *Juncus squarrosus*, *Molinia coerulea*, *Alopecurus geniculatus*.

Tinkler Fell occupies the highest point of the ridge of the Ravensworth Hills. In shape it is roughly square, rising to the highest point in the centre, which attains over 700 feet. Close to this hill is the only pond on the Fell. There are a few intermittent streams. Along the south-eastern edge was a pine plantation till recently, but this has now been felled. The Ravensworth woods are on the northern side, with a local area of heath of somewhat different type from the main Fell. Rabbits are plentiful on this part, but rare on the main portion. A few hawthorn hedges cross the Fell, giving evidence of former pasturage. In 1850, according to the ordnance survey made about that date, the north-eastern half of the Fell was under pasture, but little difference can now be detected between the two halves, except in the ribbed appearance of the ground of the part that has been ploughed.

Communities dominated by the following species occur:—*Agrostis vulgaris*, *Calluna vulgaris*, *Holcus mollis*, *Nardus stricta*, *Juncus effusus*.

II. DESCRIPTIONS OF THE ASSOCIATIONS

(1) **Dry grassland (*Agrostetum vulgaris*)** is developed at the extreme east corner of Waldrige Fell, and also dominates the pasture that overhangs this corner, just outside the Fell proper. It surrounds Pond 5, extending between the gardens of the houses and the edge of the pond. Owing to the fowls kept by the miners, manuring at this point is intense. At some points on the south-western edge it appears between the railings and the nearest path. Part of an area on the northern side, formerly enclosed as a pasture, but now disused, is covered with it, and also the disused pasture adjacent to the detached portion. It occupies in addition other pastures round the Fell. It seems probable that pasturage does actually encourage the development of this association, particularly on dry ground. The same association occurs on the drier parts of Birtley Fell, and also on a very dry and sunny bank at the north side of a pond on Tinkler Fell.

The composition of the association is as follows¹. (1) At Waldrige:—

<i>Agrostis vulgaris</i>	<i>cd</i>	<i>Rubus idaeus</i>	<i>o</i>	<i>Plantago lanceolata</i>	<i>o</i>
<i>Festuca rubra</i>	<i>cd</i>	<i>Conopodium denudatum</i>	<i>o</i>	<i>Rumex acetosella</i>	<i>o</i>
<i>Ranunculus repens</i>	<i>f</i>	<i>Galium saxatile</i>	<i>o</i>	<i>R. acetosa</i>	<i>o</i>
<i>Stellaria media</i>	<i>o</i>	<i>G. verum</i>	<i>f</i>	<i>Luzula campestris</i>	<i>f</i>
<i>Cerastium triviale</i>	<i>o</i>	<i>Hypochaeris radicata</i>	<i>o</i>	<i>Festuca ovina</i>	<i>a</i>
<i>Polygala vulgaris</i>	<i>f</i>	<i>Hieracium pilosella</i>	<i>l</i>	<i>Poa annua</i>	<i>o</i>
<i>Trifolium repens</i>	<i>a</i>	<i>Cnicus arvensis</i>	<i>f</i>	<i>P. pratensis</i>	<i>a</i>
<i>T. minus</i>	<i>r</i>	<i>C. lanceolatus</i>	<i>o</i>	<i>Dactylis glomerata</i>	<i>f</i>
<i>T. hybridum</i>	<i>r</i>	<i>Achillea millefolium</i>	<i>f</i>	<i>Holcus lanatus</i>	<i>f</i>
<i>T. procumbens</i>	<i>r</i>	<i>Crepis virens</i>	<i>r</i>	<i>H. mollis</i>	<i>o</i>
<i>Medicago lupulina</i>	<i>o</i>	<i>Leontodon autumnalis</i>	<i>o</i>	<i>Anthoxanthum odoratum</i>	<i>a</i>
<i>Potentilla fragariastrum</i>	<i>f</i>	<i>Campanula rotundifolia</i>	<i>o</i>	<i>Cynosurus cristatus</i>	<i>f</i>
<i>P. erecta</i>	<i>o</i>	<i>Calluna vulgaris</i>	<i>vr</i>	<i>Equisetum arvense</i>	<i>r</i>

(2) At Birtley:—

<i>Agrostis vulgaris</i>	<i>d</i>	<i>Genista anglica</i>	<i>r</i>	<i>Prunella vulgaris</i>	<i>o</i>
<i>Sagina procumbens</i>	<i>o</i>	<i>Rubus fruticosus</i> agg.	<i>o</i>	<i>Plantago major</i>	<i>f</i>
<i>Polygala vulgaris</i>	<i>l</i>	<i>Leontodon autumnalis</i>	<i>a</i>	<i>P. lanceolata</i>	<i>f</i>
<i>Trifolium minus</i>	<i>o</i>	<i>Bellis perennis</i>	<i>a</i>	<i>Rumex acetosella</i>	<i>a</i>
<i>T. repens</i>	<i>f</i>	<i>Taraxacum officinale</i>	<i>f</i>	<i>Luzula campestris</i>	<i>a</i>
<i>T. pratense</i>	<i>r</i>	<i>Campanula rotundifolia</i>	<i>f</i>	<i>Triodia decumbens</i>	<i>o</i>
<i>Lotus corniculatus</i>	<i>o</i>				

(3) On Tinkler Fell:—

<i>Agrostis vulgaris</i>	<i>d</i>	<i>Rumex acetosella</i>	<i>o</i>	<i>Nardus stricta</i>	<i>f</i>
<i>Trifolium minus</i>	<i>r</i>	<i>Luzula campestris</i>	<i>sd</i>	<i>Aira praecox</i>	<i>f</i>
<i>T. repens</i>	<i>vr</i>	<i>Holcus mollis</i>	<i>o</i>	<i>Poa pratensis</i>	<i>o</i>
<i>Galium saxatile</i>	<i>f</i>	<i>Festuca ovina</i>	<i>f</i>	<i>Cynosurus cristatus</i>	<i>l</i>
<i>Bellis perennis</i>	<i>vr</i>	<i>F. rubra</i>	<i>o</i>		

Along the intermittent water-courses on Birtley Fell *Agrostis* growth is stimulated; *Poa annua* and *Holcus mollis* are mixed with it. This association is clearly separated from the fringing Nardetum, which then passes into *Calluna* and Whin (*Ulex*). In places this damp Agrostetum is invaded by *Juncus squarrosus*. *Agrostis* is dominant on the greater part of Shadon's Hill. The soil is pure fine dry sand, with a very thin layer of humus.

(2) **Bracken association (*Pteridetum aquilinae*)** is at present completely dominant over all the area on Waldrige where the subsoil is dry sand; it does not attain perfect dominance except in these conditions, although in some places on sandy clay it may be seen in competition with *Ulex* and *Calluna*, and even with *Nardus*. It is not developed on Birtley Fell or Tinkler Fell, and at Beamish it is in competition with *Deschampsia flexuosa*. The species associated with the bracken are very few: where it is growing most thickly there are none at all, but where it becomes somewhat thinner *Deschampsia flexuosa*, *Vaccinium myrtillus*, or *Holcus mollis* may become subdominant. It occurs further in several of the plantations, especially in some of those on the north side of the Cong valley. From these it is capable of spreading into the surrounding land.

¹ The following contractions are used in these lists: *a*, abundant; *cd*, codominant; *d*, dominant; *f*, frequent; *l*, local; *la*, *ld*, etc., locally abundant, locally dominant, etc.; *o*, occasional; *r*, rare; *sd*, subdominant; *vr*, very rare.

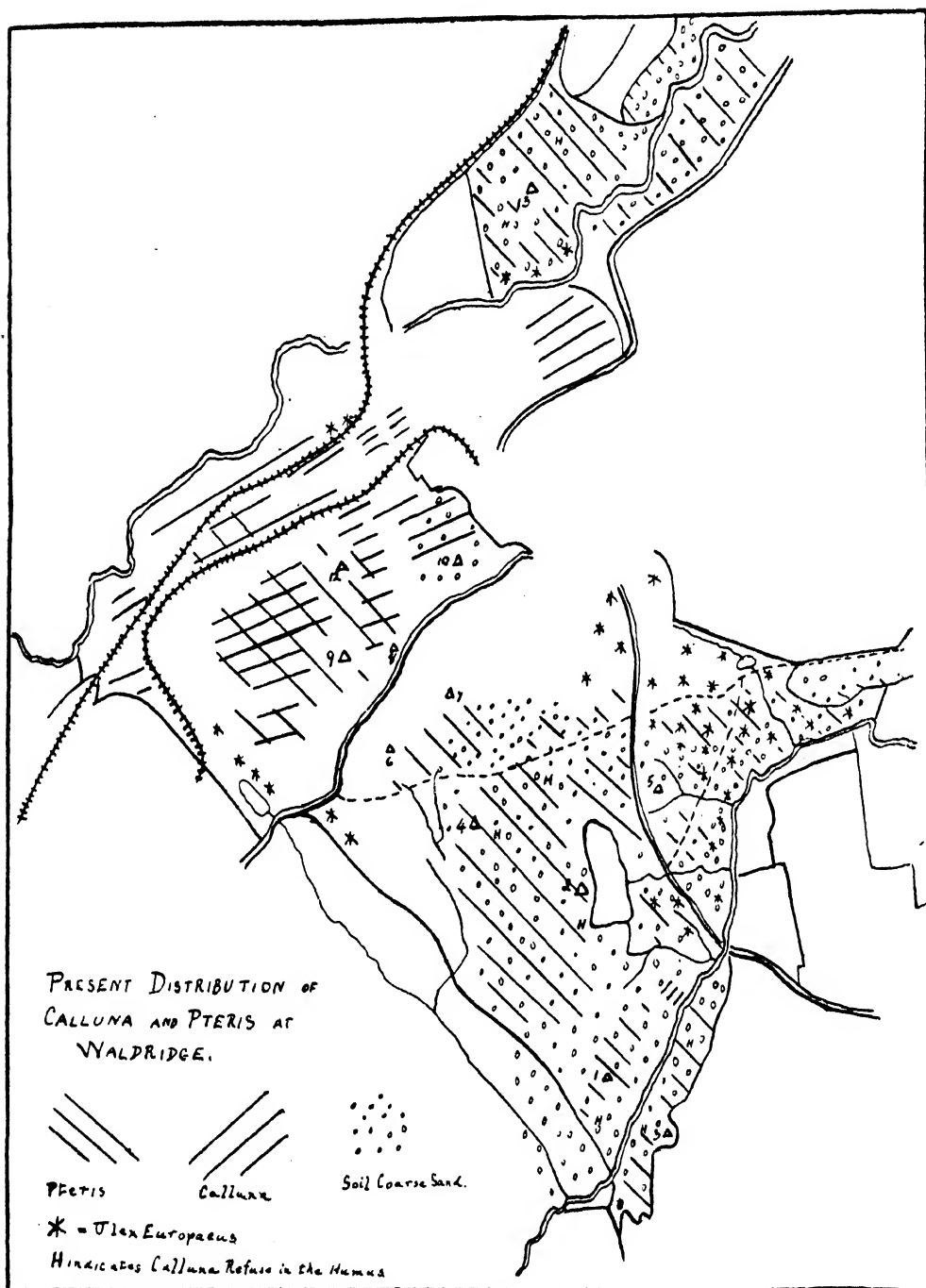


FIG. 22. Map, on the same scale as Fig. 21, showing the present distribution of *Calluna vulgaris*, *Pteris aquilina*, *Ulex europaeus*, and of coarse sandy soil.

Both of the methods of propagation of bracken (by rhizomes and by spores) are of great importance in enabling it to establish itself, but each has its limitations. In general we are safe in saying that nearly all of the new bracken stems in a continuous Pteridetum are from the rhizomes, whereas where there is a bracken patch separated by several yards from all other areas covered with the same plant the original colonisation of the outlier was due to spores. This association will be considered in greater detail later.

(3) **The Heather association (*Callunetum vulgaris*).** At present the amount of pure *Callunetum* at Waldrige (Fig. 22) is not great. There is a small patch of it beside Stream 5, and it occurs irregularly between the Cong and the main road to Chester-le-Street, on a steep slope facing north. The northern slope of Hill 10 also is nearly pure *Callunetum*. The greater part of the plateau containing Hills 9, 10 and 12 was probably originally *Callunetum*, and heather is now dominant over a very large part of it, but it appears to be degenerating, partly to bracken, partly to *Nardus*, and partly to *Molinia*. At Beamish heather is never dominant. At Birtley it occurs on a great part of the Fell, chiefly near the north end; it is nevertheless degenerating to *Ulex* and *Nardus*, and the plants are never very tall. This association reaches its greatest development on Tinkler Fell, covering more than half of it with well-grown bushes.

A peculiarity of *Calluna* is the persistence of its bark after the refuse of the plant has been buried below humus. The gradual raising of the level of the ground by deposition of vegetable matter causes considerable quantities of the dead refuse of the dominant plants to be buried in humus, though most of the material ultimately gets washed away by rain. Most of what remains rots and helps to make additional humus. It is a remarkable fact that unless *Calluna* has been actually burnt to charcoal, the bark remains in the soil in a recognisable condition long after the woody part has disappeared. I have never succeeded in identifying it, however, at a greater depth than four inches. This persistence of the refuse (even though it is not nearly so well preserved as it sometimes is in peat) makes it possible to form a very useful estimate of the former extent of the *Callunetum* on the Fells, which at Waldrige and Birtley was much greater than it now is. I have thus found *Calluna* refuse in the following places at Waldrige:—on Hill 1; on the southern slope of Hill 2; near the path just below Pond 5; and on several places on Hill 13. It has not been found near Bogs 1, 2 and 3, where *Nardetum* now occurs. *Calluna* must then have formerly grown over most of the sandy area that is now covered with bracken, and as *Calluna* now occupies all the remaining dry and sandy parts except the small area near the east corner, we may conclude that nearly all the dry sandy portion of Waldrige Fell is now or has been formerly *Calluna* heath, and much of it has since degenerated to Pteridetum. At Birtley also *Calluna* was formerly more

extensive than it is now. Explanations of this degeneration will be given later.

On the elevated part of Walldridge Fell we may see *Calluna* areas surrounded by Nardetum, in which the *Pteris* is confined to the Callunetum, none of it appearing in the Nardetum. Sometimes, but not always, there is a zone at the edge where the Callunetum is pure (*i.e.* devoid of *Pteris*). There are several obviously possible explanations of this fact. One is that we are here dealing with an incomplete zonation in the order Bracken, *Calluna*, *Nardus*, in which the factor tending to cause the dominance of bracken is not present to such an extent as to produce the full effect. Another is that the *Calluna-Nardus* separation occurred originally, and that for some reason *Pteris* was able to colonise the *Calluna* areas, but not the Nardetum. It will be shown later that the latter suggestion is sufficient to account for the fact noted, although it may not be the only factor operating.

Calluna on these hills produces a purplish-brown stain in the sand to a depth varying from 15 to 30 centimetres, but rarely seems to cement the grains so as to produce a pan, as has been recorded from other localities. The writer has observed a rather hard purplish pan several inches deep in a part of the *Ulex* area on Birtley Fell, but this does not seem to have been sufficient to prevent the *Ulex* from ousting the *Calluna* after the pan was formed.

The composition of the Callunetum is as follows:—

	Walldridge	Birtley	Tinkler Fell
<i>Ulex europaeus</i>	<i>o</i>	—	—
<i>Potentilla erecta</i>	<i>o</i>	<i>a</i>	<i>r</i>
<i>Rosa canina</i>	<i>o</i>	—	—
<i>Crataegus monogyna</i>	<i>o</i>	—	—
<i>Hieracium umbellatum</i>	—	—	<i>vr</i>
<i>Leontodon autumnalis</i>	—	—	<i>r</i>
<i>Vaccinium myrtillus</i>	<i>f</i>	<i>sd</i>	—
<i>Erica cinerea</i>	<i>f</i>	<i>a</i>	—
<i>E. tetralix</i>	—	<i>f</i>	—
<i>Empetrum nigrum</i>	<i>a</i>	—	—
<i>Luzula multiflora</i>	—	<i>f</i>	—
<i>Nardus stricta</i>	<i>f</i>	<i>a</i>	<i>f</i> to <i>cd</i>
<i>Agrostis vulgaris</i>	—	<i>f</i>	—
<i>Holcus mollis</i>	—	—	<i>f</i>
<i>Deschampsia caespitosa</i>	—	—	one plant
<i>D. flexuosa</i>	<i>la</i>	—	—
<i>Pteris aquilina</i>	<i>f</i>	—	—

(4) **Bilberry association (*Vaccinietum myrtilli*)**. This is probably a mere aspect of the Callunetum. The principal reason for separating it is that at Walldridge the bilberry continues to exist under the bracken in many places where the *Calluna* has disappeared, so that it evidently for some reason possesses greater power of resisting the destructive effect of the bracken. Its list where it occurs apparently free is as follows:—

<i>Vaccinium myrtillus</i>	<i>ld</i>	<i>Calluna vulgaris</i>	<i>a</i>	<i>Deschampsia flexuosa</i>	<i>a</i>
<i>Potentilla erecta</i>	<i>f</i>	<i>Erica cinerea</i>	<i>f</i>	<i>Agrostis vulgaris</i>	<i>f</i>

The resemblance to the Callunetum is manifest.

(5) **Deschampsietum flexuosae**. This again may represent only the degenerate residue of a number of other associations. At Waldrige it is usually to be found in a zonation at the edge of a Nardetum that is furthest from water. This correlation is very complete, but at its lower edge the Deschampsietum merges into a dry Nardetum, and may be regarded as a facies of the latter. Further, the dominant plant occurs plentifully in the Callunetum at the top of the Fell, though on the other fells it is rare in the Callunetum. Where the spread of the bracken appears to be limited at present by high water content, the *Deschampsia* is generally to be found as a narrow fringe separating the bracken from *Nardus*. This is not an invariable rule, however, and bracken frequently passes into Nardetum without any intermediate zone of *Deschampsia*.

At Beamish the nature of this association is totally different. The dominant occurs plentifully in the plantation at the north end of the Fell, as also does bracken. From this it is but a short step to assume that both these plants also occurred on what is now heathland but was formerly plantation, and that when the trees were felled they assumed local dominance, and are now struggling for the mastery under the altered conditions. The soil is a sandy clay, with humus about 8 cms. deep. At some points at Beamish I have made marks in the ground to show where the bracken front reached in the autumn of 1914, and thus to indicate the rate at which it spreads.

At Birtley *Deschampsia flexuosa* is a rare plant. It is locally dominant on some slightly elevated spots in the rolled strip but nowhere else. At Tinkler Fell the plant is never dominant.

The composition of the association is as follows:—

	Waldrige	Beamish		Waldrige	Beamish
<i>Hypericum pulchrum</i>	<i>vr</i>	—	<i>Rumex acetosella</i>	<i>o</i>	—
<i>Rubus idaeus</i>	<i>o</i>	—	<i>Salix aurita</i>	<i>l</i> (north)	—
<i>R. fruticosus</i> agg.	<i>l</i>	—	<i>Betula tomentosa</i>	—	<i>f</i>
<i>Galium saxatile</i>	<i>f</i>	<i>f</i>	<i>Scilla nutans</i>	—	<i>r</i>
<i>Solidago virga-aurea</i>	—	<i>r</i>	<i>Luzula campestris</i>	<i>r</i>	—
<i>Senecio sylvaticus</i>	—	<i>vr</i>	<i>Juncus effusus</i>	—	<i>ld</i>
<i>Campanula rotundifolia</i>	<i>l</i>	—	<i>Carex binervis</i>	<i>o</i>	<i>o</i>
<i>Erica cinerea</i>	<i>o</i>	<i>r</i>	<i>C. stellulata</i>	—	<i>r</i>
<i>E. tetralix</i>	<i>o</i> (north side)	—	<i>Festuca ovina</i>	<i>a</i>	—
	<i>vr</i> (elsewhere)		<i>F. rubra</i>	<i>f</i>	—
<i>Vaccinium myrtillus</i>	<i>r</i>	<i>a</i>	<i>Agrostis vulgaris</i>	<i>a</i>	<i>l</i>
<i>Calluna vulgaris</i>	<i>o</i> (north side)	<i>a</i>	<i>Anthoxanthum odoratum</i>	<i>o</i>	<i>vr</i>
	<i>r</i> (elsewhere)		<i>Nardus stricta</i>	<i>f</i>	<i>vr</i>
<i>Empetrum nigrum</i>	<i>l</i> (north only)	—	<i>Trisetum flavescens</i>	—	<i>o</i>
<i>Digitalis purpurea</i>	—	<i>o</i>	<i>Holcus lanatus</i>	—	<i>l</i>
<i>Teucrium scorodonia</i>	<i>l</i>	<i>l</i> (top)	<i>Aspidium spinulosum</i>	—	<i>o</i>
<i>Ilex aquifolium</i>	—	<i>vr</i>			

The number of true heath plants at Beamish is so great that it seems likely the Fell was heath before it was planted, or even that parts have never been planted at all but have always been heath. The whole area is however marked as plantation on the map of 1850.

(6) **Nardetum strictae** occurs at Walldridge under four aspects, according to the nature of the soil and the water supply. The lists vary slightly in the four cases, and these merge into each other gradually at their margins. It covers perhaps a larger area at Walldridge than any other association except bracken. It always occurs nearer to water than either bracken or *Calluna*, and it is therefore probably separated from these through having a greater water supply. In the slight depression that contains Bogs 1, 2 and 3, this is particularly well seen, for on each side the bracken is dominant: the water draining from the hills passes over the lower parts of their slopes to reach the valley, thus increasing the supply there. In these circumstances *Nardus* is found to be dominant over the whole of the valley, passing into *Juncus effusus* and *Carex goodenowii* at the bogs and streams themselves. Round the bogs the wet Nardetum may be recognised by the large quantity of *Juncus squarrosus* present. When a Nardetum is developed on coarse sand, it usually passes at its lower edge into a Moliniatum, but when the amount of clay present is large, it more frequently passes into a Juncetum effusi. The boundary is very accurately marked by the surface of the water by which the marshy areas are flooded in winter. No *Nardus* seems to grow where it is ever covered with water. Experiments are at present being carried out to test whether this correlation denotes a direct causal connection or not.

At Birtley, *Nardus* dominates most of the southern part, save where this is held by *Ulex* and *Calluna*. The northern part does not bear so much of it. In the southern portion it has certainly spread to a considerable extent at the expense of the Callunetum.

At Beamish the Nardetum does not occur. The reason is probably the historical one, that *Nardus* does not ordinarily grow in woods, and that since the plantation that formerly covered this area was cut down the *Nardus* has not yet had time to colonise the ground.

At Tinkler Fell, *Nardus* occupies a large area; indeed it and *Calluna* cover nearly all the Fell. As elsewhere, it occupies somewhat lower and accordingly damper ground than does *Calluna*.

Composition of the Nardetum

	Waldridge				Birtley	Tinkler Fell
	Fine sand and clay		Coarse sand			
	Dry	Wet	Dry	Wet		
Ranunculus flammula	—	<i>o</i>	—	—	<i>o</i>	—
Cardamine pratensis	—	—	—	—	—	<i>l</i>
Viola palustris	—	—	—	<i>l</i>	—	—
Polygala vulgaris	—	—	—	—	<i>o</i>	—
Ulex europaeus	—	—	—	—	—	<i>r</i>
Lathyrus montanus	<i>vr</i>	<i>vr</i>	—	—	—	—
Potentilla erecta	—	<i>f</i>	—	<i>f</i>	<i>f</i>	<i>f</i>
Hydrocotyle vulgaris	—	<i>a</i>	—	<i>f</i>	—	—

Composition of the Nardetum (continued)

	Waldridge				Birtley	Tinkler Fell
	Fine sand and clay		Coarse sand			
	Dry	Wet	Dry	Wet		
<i>Galium saxatile</i>	—	—	<i>a</i>	—	<i>l</i>	<i>a</i>
<i>Scabiosa succisa</i>	—	—	—	<i>l</i>	<i>f</i>	—
<i>Hieracium pilosella</i>	<i>lu</i>	—	—	—	—	—
<i>H. murorum</i>	<i>f</i>	—	—	—	—	—
<i>Cnicus paluster</i>	—	—	—	—	—	<i>f</i>
<i>Leontodon autumnalis</i>	—	—	—	—	<i>a</i>	—
<i>Achillea ptarmica</i>	—	—	—	—	<i>o</i>	—
<i>Campanula rotundifolia</i>	<i>r</i>	—	—	—	—	—
<i>Calluna vulgaris</i>	<i>o</i>	—	<i>o</i>	<i>vl</i>	<i>f to a</i>	<i>o</i>
<i>Erica tetralix</i>	—	—	—	<i>o</i>	<i>o</i>	—
<i>E. cinerea</i>	—	—	<i>o</i>	—	<i>f</i>	—
<i>Vaccinium myrtillus</i>	<i>l</i>	—	—	—	<i>o</i>	—
<i>Euphrasia officinalis</i>	—	—	—	—	<i>a</i>	—
<i>Rumex acetosella</i>	<i>r</i>	—	—	—	—	<i>r</i>
<i>Salix repens</i>	—	—	—	—	<i>f</i>	—
<i>Luzula multiflora</i>	—	<i>f</i>	—	<i>f</i>	—	<i>f</i>
<i>L. campestris</i>	<i>o</i>	—	—	—	—	—
<i>Juncus effusus</i>	—	<i>o</i>	—	—	—	<i>o</i>
<i>J. conglomeratus</i>	—	—	—	—	—	<i>o</i>
<i>J. acutiflorus</i>	—	—	—	<i>o</i>	<i>f</i>	—
<i>J. supinus</i>	—	—	—	—	<i>lsd</i>	—
<i>J. lamprocarpus</i>	—	—	—	—	<i>f</i>	—
<i>J. bufonius</i>	—	—	—	—	<i>lsd</i>	—
<i>J. squarrosus</i>	<i>cr</i>	—	<i>vr</i>	<i>f</i>	<i>ld</i>	<i>o</i>
<i>Carex leporina</i>	—	<i>o</i>	—	—	—	—
<i>C. intermedia</i>	—	—	—	<i>r</i>	—	<i>r</i>
<i>C. binervis</i>	—	—	<i>r</i>	—	<i>r</i>	—
<i>C. panicea</i>	—	<i>o</i>	—	—	—	—
<i>Festuca pratensis</i>	—	<i>r</i>	—	—	<i>f</i>	—
<i>F. ovina</i>	<i>a</i>	<i>f</i>	<i>a</i>	<i>f</i>	—	—
<i>F. rubra</i>	<i>a</i>	—	<i>o</i>	—	—	<i>f</i>
<i>Anthoxanthum odoratum</i>	—	<i>a to ld</i>	<i>o</i>	<i>a</i>	—	<i>a</i>
<i>Agrostis vulgaris</i>	<i>f</i>	—	<i>f</i>	—	<i>sd</i>	<i>f</i>
<i>Deschampsia flexuosa</i>	<i>a</i>	—	<i>sd</i>	—	—	<i>r</i>
<i>Triodia decumbens</i>	—	—	<i>f</i>	<i>f</i>	<i>f</i>	—
<i>Holcus lanatus</i>	—	<i>o</i>	—	—	<i>o</i>	—
<i>H. mollis</i>	—	—	—	<i>f</i>	—	<i>f</i>
<i>Equisetum palustre</i>	—	<i>o</i>	—	<i>o</i>	—	—

Juncus squarrosus becomes dominant on the damp ground near the south end of Birtley Fell. A peaty humus more than six inches deep occurs there. The typical Nardetum is on much drier and coarser humus, generally about three inches deep.

(7) The **Whin association (*Ulicetum europaei*)** occurs at Waldridge principally near the eastern corner, and in the disused Smithydene quarries. It is exceptionally difficult to determine to what extent *Ulex* is a native, and no definite conditions of soil and water can yet be laid down that will determine its occurrence. It grows luxuriantly high upon the pit heap (Hill 11), where the nutritive substances and the water content are both so low that only *Festuca rubra* of the ordinary heath plants seems able to grow, and that sparsely. Again, it grows on actually submerged ground in Bog 4, so that the range in which it can grow is evidently far greater than what occurs in the heath. Attempts to limit it to clay or to sand are equally fruitless.

Being a shrub, *Ulex* has the corresponding advantages and disadvantages. The principal advantages are (1) the ordinary herbaceous plants are unable to rise above it and crowd it out; (2) its lowest branches grow close to the ground, and leave little room for any herbage below, thus facilitating spreading; (3) as it is a leguminous plant, it is independent of the nitrogen supply in the soil. Its principal disadvantage, however, is that it has to regenerate itself from seed. This leads to two further defects:—(1) the seed is heavy, so that rapid spreading is difficult; (2) the young plants are herbaceous, grow slowly, and are rather sensitive.

Thus *Uliceta* somewhat resemble woodland in their ecological characters. The spread of *Ulex* must be largely determined by the facility of distribution of the seed. Viewed in this light the distribution of *Ulex* on Birtley Fell becomes of special interest. It accurately follows the wire fence that separates the Fell from the road on the eastern side; there are very few gaps, the principal being near the fork in the road. The *Ulex* area is a strip of nearly uniform width, and about fifty yards across. It is difficult to resist the opinion that in some way *Ulex* once succeeded in establishing itself either along this fence or along the disused waggon way parallel to it, and is now spreading at a fairly constant rate. A small gutter runs outside the fence, and it is possible that this may have originally served to distribute the *Ulex* seeds along its whole length. In addition to this area, *Ulex* occurs at the base of Shadon's Hill and on the Hill Pit heap. On account of the facility with which apparently bird-sown *Ulex* can colonise bare ground, it is likely that it originally established itself on the Hill Pit heap, and has since spread from that point.

On the other two fells no whin association occurs; indeed *Ulex* is there a rare plant.

The composition of the association is as follows:—

	Waldridge	Birtley		Waldridge	Birtley
<i>Ranunculus repens</i>	<i>o</i>	<i>o</i>	<i>Hypochaeris radicata</i>	<i>f</i>	<i>f</i>
<i>R. flammula</i>	—	<i>o</i>	<i>Erica cinerea</i>	<i>r</i>	<i>o</i>
<i>Viola sylvestris</i>	<i>o</i>	—	<i>Calluna vulgaris</i>	—	<i>o</i>
<i>Linum catharticum</i>	—	<i>l</i>	<i>Digitalis purpurea</i>	<i>o</i>	—
<i>Stellaria holostea</i>	<i>r</i>	—	<i>Teucrium scorodonia</i>	<i>f</i>	—
<i>S. graminea</i>	<i>o</i>	—	<i>Rumex acetosella</i>	<i>f</i>	<i>a</i>
<i>Cerastium triviale</i>	—	<i>o</i>	<i>Salix repens</i>	—	<i>f to lsd</i>
<i>Genista anglica</i>	—	<i>r</i>	<i>Luzula multiflora</i>	—	<i>o</i>
<i>Rubus fruticosus</i> agg.	<i>f</i>	—	<i>Juncus effusus</i>	—	<i>f</i>
<i>R. idaeus</i>	<i>f</i>	—	<i>Carex goodenowii</i>	—	<i>o</i>
<i>Rosa canina</i>	<i>r</i>	—	<i>C. flava</i>	—	<i>l</i>
<i>Potentilla erecta</i>	<i>r</i>	<i>a</i>	<i>C. leporina</i>	—	<i>r</i>
<i>Pimpinella saxifraga</i>	<i>o</i>	—	<i>Agrostis vulgaris</i>	—	<i>a</i>
<i>Galium saxatile</i>	<i>f</i>	—	<i>Anthoxanthum odoratum</i>	<i>a</i>	<i>o</i>
<i>Scabiosa succisa</i>	—	<i>f</i>	<i>Holcus mollis</i>	<i>f</i>	<i>f</i>
<i>Achillea ptarmica</i>	—	<i>o</i>	<i>H. lanatus</i>	—	<i>a</i>
<i>Solidago virga-aurea</i>	<i>l</i>	<i>l</i>	<i>Molinia coerulea</i>	—	<i>f</i>
<i>Senecio jacobaea</i>	—	<i>l</i>	<i>Pteris aquilina</i>	<i>f</i>	<i>vr</i>
<i>Oniscus arvensis</i>	<i>f</i>	—	<i>Aspidium spinulosum</i>	<i>r</i>	—
<i>C. paluster</i>	<i>r</i>	<i>f</i>	<i>Ophioglossum vulgatum</i>	<i>vr</i>	—
<i>Hieracium murorum</i>	<i>r</i>	—	<i>Equisetum arvense</i>	—	<i>vr</i>
<i>H. umbellatum</i>	<i>vr</i>	—			

(8) **Holcetum mollis.** This association occurs in scattered patches in many parts of Walldridge Fell. The principal is in a slight depression near the summit of Hill 13, where its development is due apparently to the presence of rabbits, which attack this plant less than almost any other. It also occurs in many parts of the lower slopes of hills at both Walldridge and Beamish. The dominant covers most of the ground in many of the plantations, but seems to be sharply limited where the slope becomes steep. Steep slopes in plantations and woods are generally tenanted by *Pteris*, *Deschampsia flexuosa* and *Aspidium filix-mas*. *Holcus mollis* also grows under all the hawthorn bushes at the base of the Cong Valley, although these are surrounded by *Deschampsia flexuosa*. It is locally dominant on the west side of Shadon's Hill, on some damp places of small gradient. From these facts it appears likely that a large quantity of organic matter in the soil tends to favour *Holcus mollis*; this has since been verified experimentally. In addition, this plant is among the first to colonise a burnt area, and it is favoured by shade, at the expense of its ordinary competitors. Its ecological relations are thus very complicated. In the absence of all the disturbing factors that favour it, it is unable to hold its own, but when they enter, it becomes a very important member of the ground flora.

The *Holcetum mollis* of summit of Hill 13 has *Potentilla procumbens* o, *Rubus fruticosus* agg. r, *Galium saxatile* a, *Calluna vulgaris* r, *Urtica dioica* r, *Juncus effusus* o, *J. squarrosus* o; while under the hawthorn bushes the ground vegetation consists of *Viola sylvestris* o, *Lychnis diurna* o, *Senecio sylvaticus* 1 plant, *Digitalis purpurea* 1 plant, *Agrostis vulgaris* f, *Holcus mollis* cd, *Pteris aquilina* cd. The violet and the campion here mentioned occur also sparingly under the bracken near by.

(9) **Molinietum coeruleae** occurs principally round the outlet of the Wanister bog. It is developed on a fairly deep stratum intermediate in character between humus and peat. The damper parts merge into an association of **Carex goodenowii**, but the transition is gradual, and too much reliance must not be placed on the separation into two associations. It occurs again in the depression that surrounds Hill 9, and in one bog on the northern slope; this bog is peculiar in that *Narthecium ossifragum* is subdominant. All these spots are either in depressions or else supplied with water with a high content of organic matter; the water content and the organic content are therefore both presumably higher than in the surrounding parts, which are generally *Nardetum*. In a small bog near the Chester Moor road *Carex goodenowii* is in almost pure dominance.

The associations are composed of the following species:—

Molinietum Caricetum		Molinietum Caricetum	
Ranunculus flammula	o	Lotus major	f
Cardamine pratensis	r	Potentilla erecta	o
Viola palustris	f	Hydrocotyle vulgaris	f
Sagina nodosa	—	Galium uliginosum	—
	f		f

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	Molinietum	Caricetum		Molinietum	Caricetum
<i>Valeriana dioica</i>	—	<i>f</i>	<i>Narthecium ossifragum</i>	<i>r to lsd</i>	—
<i>Scabiosa succisa</i>	<i>f</i>	<i>a</i>	<i>Triglochin palustre</i>	<i>f</i>	—
<i>Cnicus paluster</i>	<i>f</i>	—	<i>Carex goodenowii</i>	<i>a</i>	<i>d</i>
<i>Achillea ptarmica</i>	—	<i>o</i>	<i>C. stellulata</i>	<i>o</i>	<i>sd</i>
<i>Calluna vulgaris</i>	<i>lf</i>	—	<i>C. panicea</i>	<i>o</i>	<i>a</i>
<i>Erica tetralix</i>	<i>lf</i>	—	<i>C. flava</i>	—	<i>a</i>
<i>Empetrum nigrum</i>	<i>lf</i>	—	<i>C. pulicaris</i>	—	<i>vr</i>
<i>Menyanthes trifoliata</i>	—	<i>a</i>	<i>Anthoxanthum odoratum</i>	<i>a to ld</i>	—
<i>Anagallis tenella</i>	—	<i>r</i>	<i>Nardus stricta</i>	<i>f</i>	—
<i>Pinguicula vulgaris</i>	—	<i>f</i>	<i>Festuca ovina</i>	<i>o</i>	—
<i>Juncus supinus</i>	—	—	<i>Molinia coerulea</i>	<i>d</i>	—
<i>var. fluitans</i>	—	<i>o</i>	<i>Holcus lanatus</i>	—	<i>f</i>
<i>J. obtusiflorus</i>	—	<i>f</i>	<i>Briza media</i>	—	<i>o</i>
<i>J. squarrosus</i>	<i>o</i>	—	<i>Aspidium spinulosum</i>	—	<i>l</i>
<i>Luzula multiflora</i>	<i>o</i>	<i>o</i>	<i>Equisetum sylvaticum</i>	—	<i>l</i>
<i>Scirpus caespitosus</i>	—	<i>f</i>	<i>Sphagnum</i> spp.	—	<i>o</i>
<i>Orchis ericetorum</i>	—	<i>f</i>			

(10) **Oak-Hazel Wood** occurs on the steep slope (in some places quite precipitous) on the northern slope of the Fell. The soil is a sandy clay, and usually very dry, except where intermittent streams are running. The exposed rocks are a hard jointed shale. Most of the trees are small, and none exceed 30 feet. List:—*Quercus sessiliflora* *sd*, *Corylus avellana* *d*, *Betula alba* *ld*, *Crataegus monogyna* *f*, *Rosa canina* *f*, *Fraxinus excelsior* *r*, *Holcus lanatus* *f*, *Deschampsia flexuosa* *f*.

On a level part of the bank just above this wood, *Salix aurita* occurs in large quantity, and with it its hybrids with *S. caprea* and *S. cinerea*. Only one plant of pure *S. caprea* has been found. A dry Nardetum surrounds this thicket. A somewhat similar thicket occurs on a flat part at the base of the hill, where the following occur:—*Salix aurita* *a*, *S. caprea* 1 plant, *S. cinerea* 2 plants, *Holcus mollis* *d*, *Festuca pratensis* *a*, *Agrostis vulgaris* *a*, *Pteris aquilina* *f*.

(11) **Hawthorn Scrub.** On the steep slope of the detached portion, where landslips are frequently occurring, an open hawthorn scrub is developed. The soil is fine sand, which is full of small apparently water-worn boulders at the top. List:—*Ulex europaeus* *f*, *Cytisus scoparius* *o*, *Crataegus monogyna* *d*, *Rosa dumetorum* *o*, *R. villosa* *vr*, *Rubus idaeus* *o*, *Sambucus niger* *f*, *Fraxinus excelsior* (young) *o*, *Agrostis vulgaris* *sd*, *Holcus mollis* *f*, *Deschampsia flexuosa* *sd*, *Pteris aquilina* *sd*. The very small stream numbered 14 has many hawthorn bushes on its banks; very few occur among the surrounding bracken.

(12) **Marsh associations.** Examples of these in this area are nine in number, and little more than a sketch of them will be given here. The alder, birch, and *Salix cinerea* woods may also be included in this section. As there seems to be little necessary ecological connection between marshes that are not connected by watercourses, the simplest mode of treatment is to deal with them geographically in a convenient order.

Bog 4, near the most easterly corner of Waldrige Fell, differs from all the other marshes in the comparative purity of its water, which is almost

colourless. Stream 10, which flows through it, is a rapid stream and appears to be deep-seated, as it never becomes dry even in summer. An analysis of the water of the bog was made in June, 1915, to find the organic matter, the acidity, and the dissolved oxygen. Only a rough titration with permanganate and sulphuric acid was made to find the reducing strength of the organic matter present. The dissolved oxygen was found by Winkler's method¹. It was found that the reducing strength was equivalent to less than $\frac{1}{1000}$ normal permanganate, the dissolved oxygen amounted to 2.6 c.c. per litre, and the acidity, estimated with caustic soda and phenolphthalein, was $3.4 \times N \times 10^{-4}$. The mineral content is low in all the waters examined, and is mainly due to iron.

The centre of this bog and that of the upper part of the issuing stream are dominated by a dense growth of *Epilobium hirsutum*. No other plant grows among it. Round the edges a different association occurs in the shallow water, dominated by *Juncus glaucus*. The composition of this in the bog is as follows:—

<i>Ranunculus repens</i>	<i>a</i>	<i>Ulex europæus</i>	1 bush	<i>Senecio aquaticus</i>	<i>o</i>
<i>R. flammula</i>	<i>o</i>	<i>Epilobium tetragonum</i>		<i>Mentha aquatica</i>	<i>a</i>
<i>Nasturtium officinale</i>	<i>a</i>	var. <i>obscurum</i>	<i>o</i>	<i>Poa trivialis</i>	<i>a</i>
<i>Cardamine pratensis</i>	<i>r</i>	<i>Ulmaria palustris</i>	<i>o</i>	<i>Deschampsia caespitosa</i>	<i>f</i>
<i>C. flexuosa</i>	<i>r</i>	<i>Galium palustre</i>	<i>f</i>	<i>Carex goodenowii</i>	<i>o</i>
<i>Cerastium triviale</i>	<i>f</i>	<i>Cnicus paluster</i>	<i>f</i>	<i>Equisetum palustre</i>	<i>o</i>
<i>Lotus major</i>	<i>f</i>	<i>Tussilago farfara</i>	<i>o</i>		

Round the outlet the vegetation is not so close, and the only plants growing are *Nasturtium officinale* sd; *Glyceria fluitans* lsd; *Ranunculus lenormandi* a.

The plants associated with *Juncus glaucus* in the upper part of the stream are very different. They are:—*Ranunculus repens*, *Stellaria uliginosa*, *Hydrocotyle vulgaris*, *Senecio aquaticus*, *Veronica beccabunga*, *Stachys sylvatica*, *Myosotis caespitosa*, *Holcus lanatus*, *Triglochin palustre*.

On the margin of the stream is a fringe of *Juncus acutiflorus*, merging to *Scirpus palustris* lower down, with *Equisetum limosum* occasional and *Lychnis flos-cuculi* frequent.

Bog 7, near the most westerly corner of the Fell, lies at the bottom of an almost precipitous slope. The soil under it seems to be clay, while the water does not seem much different from that in Bog 4. The vegetation, however, is altogether different:—*Sparganium ramosum* d, *Ranunculus flammula* f, *Cardamine pratensis* o, *Galium uliginosum* f, *Veronica scutellata* o, *Potamogeton natans* a, *Eleocharis palustris* a, *Glyceria fluitans* sd, *Equisetum limosum* sd, *Sphagnum* sp. a. *Juncus effusus* is dominant round the edge. This vegetation is very similar to that of the ponds in disused clay-fields in the same district.

Pond 13 is supplied with water from the boilers of the colliery engines,

¹ Purvis and Hodgson, *Water, Sewage, and Foods*, Cambridge, 1914, p. 46.

and cannot be regarded as natural. In it *Glyceria fluitans* and *Alopecurus geniculatus* are co-dominant.

Bogs 1, 2, 3, 6, 9, 10, and 12 are all occupied by *Juncus effusus*. The water of all of them is stagnant while it is present, but usually dries up in summer. There is no underlying peat. The associated species are few, the chief being *Juncus bufonius*, *Carex goodenowii* and *Agrostis alba*. The last is locally dominant round the margin of Pond 10.

Streams 8 and 9, and most of the other intermittent streams, have their beds covered with a wet Nardetum, with *Anthoxanthum*, *Deschampsia caespitosa*, *Carex panicea*, *C. flava*, and *Hydrocotyle*. In many places *Juncus effusus* occurs in the centre. Its leaves are very dry in summer, and much bracken grows among it. Nearly all this bracken has the ends of its leaves withered. No bracken occurs in the Nardetum, although it is usually dominant on the other side of the Nardetum.

The sides of the South Burn above the Chester Moor entrance are lined with spontaneous woods of *Alnus rotundifolia*, *Salix cinerea* and *Betula alba*. The alder occupies most of the left bank to a distance of about 30 metres from the stream. The soil is very wet, with a large amount of organic matter. The flora is very rich. List:—

<i>Ranunculus repens</i>	<i>f</i>	<i>Scrophularia nodosa</i>	<i>o</i>
<i>R. flammula</i>	<i>f</i>	<i>Veronica chamocedrys</i>	<i>o</i>
<i>Lychnis dioica</i>	<i>f</i>	<i>Digitalis purpurea</i>	<i>f</i>
<i>Hypericum tetrapterum</i>	<i>o</i>	<i>Pedicularis palustris</i>	<i>a</i>
<i>Geranium robertianum</i>	<i>o</i>	<i>Ajuga reptans</i>	<i>o</i>
<i>Acer pseudoplatanus</i>	<i>r</i>	<i>Stachys sylvatica</i>	<i>o</i>
<i>Oxalis acetosella</i>	<i>f</i>	<i>Prunella vulgaris</i>	<i>f</i>
<i>Trifolium repens</i>	<i>f</i>	<i>Mentha aquatica</i>	<i>f</i>
<i>Lotus major</i>	<i>f</i>	<i>Lysimachia nemorum</i>	<i>o</i>
<i>Vicia cracca</i>	<i>o</i>	<i>Alnus rotundifolia</i>	<i>d</i>
<i>Crataegus oxyacantha</i>	<i>f</i>	<i>Salix cinerea</i>	<i>sd</i>
<i>Spiraea ulmaria</i>	<i>f</i>	<i>S. caprea</i>	<i>rr</i>
<i>Pyrus aucuparia</i>	<i>f</i>	<i>S. aurita</i>	<i>a</i>
<i>Rosa canina</i>	<i>o</i>	<i>S. pentandra</i>	<i>a</i>
<i>Rubus idaeus</i>	<i>f</i>	<i>Rumex conglomeratus</i>	<i>f</i>
<i>Epilobium palustre</i>	<i>o</i>	<i>Juniperus communis</i>	<i>f</i>
<i>Chrysosplenium oppositifolium</i>	<i>o</i>	<i>Callitriche</i> sp.	<i>o</i>
<i>Oenanthe crocata</i>	<i>o</i>	<i>Orchis maculata</i>	<i>f</i>
<i>Galium cruciatum</i>	<i>f</i>	<i>Juncus effusus</i>	<i>o</i>
<i>G. palustre</i>	<i>o</i>	<i>Luzula sylvatica</i>	<i>f</i>
<i>Viburnum opulus</i>	<i>a</i>	<i>Carex vulpina</i>	<i>f</i>
<i>Lonicera periclymenum</i>	<i>f</i>	<i>C. leporina</i>	<i>f</i>
<i>Valeriana dioica</i>	<i>f</i>	<i>C. laevigata</i>	<i>f</i>
<i>V. officinalis</i>	<i>f</i>	<i>C. paniculata</i>	<i>a</i>
<i>Eupatorium cannabinum</i>	<i>a</i>	<i>Glyceria fluitans</i>	<i>o</i>
<i>Lapsana communis</i>	<i>f</i>	<i>Holcus mollis</i>	<i>a</i>
<i>Solidago virga-aurea</i>	<i>f</i>	<i>Deschampsia caespitosa</i>	<i>a</i>
<i>Menyanthes trifoliata</i>	<i>la</i>	<i>Equisetum sylvaticum</i>	<i>a</i>
<i>Fraxinus excelsior</i>	<i>o</i>	<i>Aspidium filix-mas</i>	<i>f</i>

On the other bank most of the ground is occupied by a rather open birch wood, with *Holcus mollis* or *Deschampsia caespitosa* subdominant, according to the dampness of the soil. The rest is covered with *Salix cinerea*, but the ground flora is so similar to that of the alder wood that it seems possible that the willow thicket may have only arisen in consequence of the partial

felling of a previously existing alder wood¹. Some alder trees still stand. All these woods are confined to the base of the hills, and cease abruptly where the gradient becomes great.

On Birtley Fell there are few, if any, natural streams, but numerous ditches have been cut. These have a characteristic vegetation, of a very open type. The water is fairly pure, but acid. List:—

<i>Ranunculus flammula</i>	<i>a</i>	<i>Senecio aquaticus</i>	<i>a</i>
<i>Cardamine pratensis</i>	<i>a</i>	<i>Myosotis caespitosa</i>	<i>f</i>
<i>Sagina procumbens</i> agg.	<i>f</i>	<i>Veronica buxbaumii</i>	<i>o</i>
<i>S. nodosa</i>	<i>l</i>	<i>Juncus effusus</i>	<i>f</i>
<i>Stellaria media</i>	<i>ld</i>	<i>J. lamprocarpus</i>	<i>f</i>
<i>S. uliginosa</i>	<i>l</i>	<i>J. obtusiflorus</i>	<i>f</i>
<i>Lotus major</i>	<i>f</i>	<i>Carex panicea</i>	<i>l</i>
<i>Peplis portula</i>	<i>l</i>	<i>C. flava</i>	<i>l</i>
<i>Hydrocotyle vulgaris</i>	<i>f</i>	<i>Poa annua</i>	<i>f</i>
<i>Gnaphalium uliginosum</i>	<i>f</i>	<i>Agrostis alba</i>	<i>ld</i>
<i>Cnicus paluster</i>	<i>a</i>		

In the true bogs a different association occurs, resembling most the *Glyceria* pond at Walldridge, although it is more natural. List:—

<i>Ranunculus dronetii</i>	<i>ld</i>	<i>Juncus effusus</i>	<i>f</i>	<i>Scirpus setaceus</i>	<i>l</i>
<i>R. lenormandi</i>	<i>l</i>	<i>J. conglomeratus</i>	<i>f</i>	<i>Alopecurus geniculatus</i>	<i>l</i>
<i>Helosciadium inundatum</i>	<i>l</i>	<i>J. supinus</i>	<i>f</i>	<i>Glyceria fluitans</i>	<i>f</i>
<i>Myosotis caespitosa</i>	<i>f</i>	<i>Carex panicea</i>	<i>f</i>	<i>Sphagnum</i> sp.	<i>j</i>
<i>Juncus bufonius</i>	<i>a</i>	<i>C. flava</i>	<i>f</i>		

The small meres contain very peaty water. The vegetation of their beds consists mainly of *Carex goodenowii* and *C. panicea*; *Juncus squarrosus*, *Calluna* and *Nardus* occur round the edges. Usually no true water plants occur, but sometimes *Ranunculus flammula* and the wet-growing form of *Agrostis alba* are to be found in the bottom when the water has nearly dried up. The sides are sometimes lined with *Molinia*, *Erica tetralix*, and *Juncus squarrosus* above the level of the water, while *Nardus* and *Calluna* come down to the upper edge of the *Molinia* zone.

Wanister Bog (Bog 11) is the largest of the Walldridge bogs. It occupies the flat ground to the east of the Wanister Hill, and varies considerably in size during the year. It is smallest in September, and largest in May. When it is fullest the depth may reach half a metre, but sometimes the whole becomes dry. The water is brown and strongly acid. An analysis in June, 1915, showed that the reducing strength was $\frac{N}{200}$, the dissolved oxygen 2.1 c.c. per litre, and the acidity $13.2 \times N \times 10^{-4}$. The principal inlets are intermittent streams dominated by *Juncus effusus*. The bog itself is full of the unbranched form of *Equisetum limosum*.

The list of the association is as follows:—

<i>Ranunculus flammula</i>	<i>o</i>	<i>Menyanthes trifoliata</i>	<i>f</i>	<i>Carex goodenowii</i>	<i>a</i>
<i>R. repens</i>	<i>f</i>	<i>Juncus supinus</i>	<i>f</i>	<i>C. stellulata</i>	<i>o</i>
<i>Epilobium palustre</i>	<i>o</i>	<i>Potamogeton plantagineus</i>	<i>a</i>	<i>Equisetum limosum</i>	<i>d</i>
<i>Hydrocotyle vulgaris</i>	<i>a</i>	<i>Eriophorum angustifolium</i>	<i>o</i>	<i>Sphagnum</i> sp.	<i>sd</i>

¹ Compare **Tansley, A. G.**, *Types of British Vegetation*, Cambridge, 1911.

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The cotton-sedge ten years ago was vastly more plentiful than it is now. The bottom of the bog is pure peat, and is very powdery when the water dries up. Much marsh gas rises from the decomposing matter at the bottom. Where the *Eriophorum* grows the depth in June, 1915, was about 15 cms. The *Equisetum* all over the bog rose a uniform 40 cms. above the surface of the water. About August all the stems of this plant die and collapse.

At the top end of the bog is a *Caricetum goodenowii* of the following composition:—

<i>Ranunculus flammula</i>	<i>f</i>	<i>Carex goodenowii</i>	<i>d</i>
<i>R. repens</i>	<i>f</i>	<i>C. stellulata</i>	<i>f</i>
<i>Cardamine pratensis</i>	<i>f</i>	<i>Scirpus setaceus</i>	<i>o</i>
<i>Hydrocotyle vulgaris</i>	<i>sd</i>	<i>Anthoxanthum odoratum</i>	<i>a</i>
<i>Cnicus paluster</i>	<i>o</i>	<i>Festuca pratensis</i>	<i>o</i>
<i>Menyanthes trifoliata</i>	<i>a to sd</i>	<i>F. rubra</i>	<i>vr</i>
<i>Juncus effusus</i>	<i>f</i>	<i>Holcus lanatus</i>	<i>o</i>
<i>J. acutiflorus</i>	<i>a</i>	<i>Equisetum limosum</i>	<i>a</i>
<i>Luzula multiflora</i>	<i>o</i>		

Streams 5 and 7 have their sources in this bog. Most of their length is occupied by an association dominated by *Juncus acutiflorus*. The streams are moving rapidly where this occurs, and most of the plants grow with their roots permanently submerged. List:—

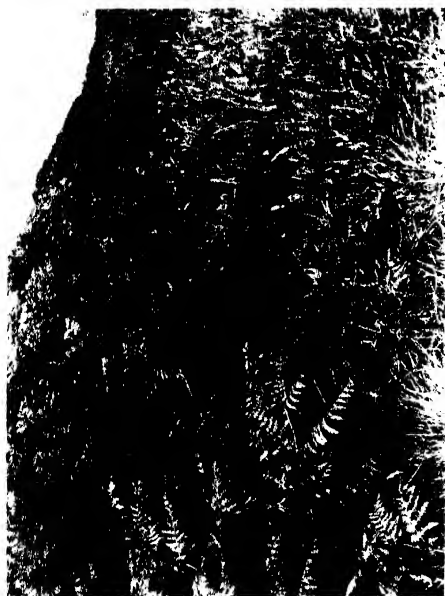
<i>Ranunculus acer</i>	<i>o</i>	<i>Juncus obtusiflorus</i>	<i>f</i>
<i>R. repens</i>	<i>o</i>	<i>Eriophorum angustifolium</i>	<i>r</i>
<i>R. flammula</i>	<i>f</i>	<i>Carex flava</i>	<i>o</i>
<i>Cardamine pratensis</i>	<i>r</i>	<i>C. panicea</i>	<i>f</i>
<i>Hydrocotyle vulgaris</i>	<i>a</i>	<i>C. stellulata</i>	<i>f</i>
<i>Taraxacum officinale</i>	<i>o</i>	<i>C. goodenowii</i>	<i>a to ld</i>
<i>Cnicus paluster</i>	<i>o</i>	<i>Glyceria fluitans</i>	<i>f</i>
<i>Triglochin palustre</i>	<i>f</i>	<i>Festuca rubra</i>	<i>o</i>
<i>Juncus acutiflorus</i>	<i>d</i>	<i>Anthoxanthum odoratum</i>	<i>f</i>
<i>J. lamprocarpus</i>	<i>f</i>	<i>Equisetum limosum</i>	<i>ld</i>
<i>J. supinus</i> with <i>v. fluitans</i>	<i>o</i>	<i>E. palustre</i>	<i>f</i>

At the edges this association passes into a *Molinietum*, and then to *Calluna* and bracken.

A different *Juncetum effusi*, with many associated species, occurs in the lower part of Stream 7, the composition being as follows:—

<i>Ranunculus acer</i>	<i>f to a</i>	<i>Cnicus arvensis</i>	<i>f</i>
<i>Caltha palustris</i>	<i>f</i>	<i>Mentha aquatica</i>	<i>f</i>
<i>Cardamine pratensis</i>	<i>a</i>	<i>Ajuga reptans</i>	<i>f</i>
<i>Viola palustris</i>	<i>f</i>	<i>Rumex acetosa</i>	<i>o</i>
<i>Vicia cracca</i>	<i>o</i>	<i>Salix cinerea</i>	<i>o</i>
<i>Ulmaria palustris</i>	<i>a</i>	<i>Orchis ericetorum</i>	<i>o</i>
<i>Hydrocotyle vulgaris</i>	<i>a</i>	<i>Juncus effusus</i>	<i>d</i>
<i>Angelica sylvestris</i>	<i>o</i>	<i>J. glaucus</i>	<i>f</i>
<i>Valeriana officinalis</i>	<i>f</i>	<i>J. acutiflorus</i> (at margin)	<i>ld</i>
<i>Crepis paludosa</i>	<i>r</i>	<i>Carex remota</i>	<i>o</i>
<i>Tussilago farfara</i>	<i>o</i>	<i>Aspidium spinulosum</i>	<i>f</i>
<i>Cnicus paluster</i>	<i>f</i>		

The marginal association is the wet *Nardetum*. Where the gradient is very small, *Eleocharis palustris* becomes dominant. The same plant is dominant where Stream 5 spreads out into a broad spongy bog, but the associated species are totally different.



Phot. 1



Phot. 2



Phot. 3

Phot. 4

JEFFREYS—ON THE VEGETATION OF FOUR DURHAM COAL-MEASURE FELS (pp. 174--195).

The Scirpetum of the slowly moving stream includes :

<i>Ranunculus repens</i>	<i>f</i>	<i>Taraxacum officinale</i>	<i>r</i>	<i>Eriophorum angustifolium</i>	<i>vr</i>
<i>R. flammula</i>	<i>f</i>	<i>Ononis paluster</i>	<i>f</i>	<i>Deschampsia caespitosa</i>	<i>o</i>
<i>Rubus idaeus</i>	<i>a</i>	<i>Juncus glaucus</i>	<i>l</i>	<i>Glyceria fluitans</i>	<i>a</i>
<i>Hydrocotyle vulgaris</i>	<i>a</i>	<i>J. effusus</i>	<i>a</i>	<i>Equisetum palustre</i>	<i>a</i>

The Scirpetum of the acid bog includes :

Cardamine pratensis	Valeriana dioica	Salix cinerea	
Lychnis flos-cuculi	Crepis paludosa	Orchis ericetorum	
Angelica sylvestris	Senecio aquaticus	Juncus glaucus	l
Galium palustre	Menyanthes trifoliata	J. acutiflorus	cd
G. uliginosum	Myosotis palustris	Eleocharis palustris	cd
Valeriana officinalis	Pinguicula vulgaris		

The study of the numerous constituent associations of the marsh formation thus appears to be a matter of considerable complexity. It appears probable however that the following suggestions may afford a useful basis of subsequent investigation.

- (1) A clay soil, permanently submerged, tends to favour *Sparganium ramosum*.
- (2) Ground that is very wet, usually submerged, in winter, and badly drained, or else supplied with water with a high content of organic matter, favours *Juncus effusus*.
- (3) More rapid drainage, combined with a higher supply of organic matter, favours *Juncus acutiflorus*.
- (4) Deeper water of the same type as the last favours *Equisetum limosum*.
- (5) Shallow water, with a very small amount of organic matter, or acid, favours *Juncus glaucus*.
- (6) Somewhat deeper water of the same type favours *Epilobium hirsutum*.
- (7) A less permanent supply of pure water favours *Glyceria aquatica* and *Alopecurus geniculatus*.
- (8) Slowly moving permanent acid streams and a very wet type of acid bog favour *Eleocharis palustris*.

The material available is inadequate to establish whether these relations are general. They account adequately for the distribution of the herbaceous associations of the marsh formation in the areas considered, and do not appear to be contradicted by observations elsewhere. Until more detailed treatment, preferably by experiment, is possible, they are offered tentatively as the simplest set of hypotheses that satisfy the observed conditions.

DESCRIPTION OF PHOTOGRAPHS ON PLATE XI

- Phot. 1. Zonation at Stream 10. *Juncus glaucus* in bed of stream, with *Nardus* at the edges. On the left this passes to *Ulex* and then to *Deschampsia flexuosa* and *Pteris aquilina*. Bog 4, with *Epilobium hirsutum*, is just visible in the background.
- Phot. 2. Base of Wanister Hill (Hill 2). Bracken dominates the slope, and is cut off sharply at the bottom, where it changes to *Holcus lanatus*.
- Phot. 3. Zonation beside the Wanister Bog. Bracken on the right, *Juncus acutiflorus* in the edge of the bog on the left, with a light coloured intermediate zone of *Nardus*. The grass with the conspicuous white heads is *Anthoxanthum odoratum*.
- Phot. 4. The Wanister Bog, with Hill 4 behind it. Pale area of *Equisetum limosum* in the centre, passing to *Eleocharis palustris*, and then to *Carex goodenowii* with *Juncus acutiflorus*. *Potamogeton plantagineus* occurs in the open area in the foreground. On the hill behind, the upper part is dominated by bracken, and the lower by *Nardus*, with some *Juncus effusus* in the beds of the streams.

NOTICE OF PUBLICATION ON FOREIGN VEGETATION

W. S. Cooper. "Plant Succession in the Mount Robson Region, British Columbia." *The Plant World*, **19**, 1916, pp. 211-238, 8 text-figures (photographs).

Mount Robson is situated upon the eastern edge of British Columbia, overlooking the Continental Divide. "Although the mountain is but six miles from the tracks of the Grand Trunk Pacific and Canadian Northern Railroads, it is almost upon the northern edge of the known country. Beyond it lie hundreds of miles of mountains as yet unmapped, and hardly even penetrated." Precipitation is heavy and well distributed through the year, but no climatic records are known. The effects of present and past glaciation and of post-glacial weathering are apparent everywhere, and these are the controlling physiographic factors in reference to vegetation.

There are three vegetational and presumably climatic zones: (1) the montane zone (forest climax), (2) the sub-alpine zone (forest climax), and (3) the alpine zone (alpine meadow, rock and snow). The last mentioned was not studied by the author.

The montane zone has an upper limit of 3500 feet (1077 metres). This bears climax forest very similar to that of the lower zone of the Selkirk Mountains (Pacific Coast type) and is composed of *Thuja plicata* (most abundant), *Picea Engelmanni*, *Abies lasiocarpa*, *Tsuga heterophylla* and *Pseudotsuga mucronata*. The young tree growth is mainly *Abies* and *Thuja*. The shrub layer includes *Acer glabrum*, *Azaleastum albiflorum*, *Menziesia ferruginea* and locally *Fatsia horrida*. The herbaceous layer includes *Phegopteris Dryopteris*, *Equisetum sylvaticum*, *Clintonia uniflora*, *Moneses uniflora* and *Pyrola uliginosa*. Mosses are abundant. This zone is unfavourable for the study of successions because of the almost total destruction of the primitive habitats—rock surfaces and moraines. The bulk of the territory is now divided between rocky and talus covered slopes and shingle flats. On the slopes the climax forest makes almost continuous cover; on the shingle flats there are tracts of mature climax forest, but stages of succession are common because of the continual erosional and depositional activities of the rivers.

The subalpine zone has an upper limit of 6500 feet (2000 metres). *Picea Engelmanni* is dominant in the climax forest and is accompanied by *Abies lasiocarpa* and *Pinus albicaulis*. Young growth is mainly *Abies*, which layers abundantly. This forest is much poorer in species and in the size of trees, than that of the montane zone, and the difference consists rather in the elimination of certain species important in the lower than in the complete substitution of species. The absence of *Tsuga*, *Pseudotsuga*, *Thuja* and *Fatsia* profoundly changes the aspect and character of the forest. *Tsuga*, *Thuja* and *Fatsia* are distinctively Pacific Coast species, while the *Picea* and *Abies* belong almost as distinctively to the Rocky Mountain region. Among the accompanying plants are *Menziesia ferruginea*, *Cassiope mertensiana*, *Moneses uniflora*, *Pyrola chlorantha*, *P. uliginosa*, *Phyllo-doce glandulifera*, *P. intermedia*, *P. empetriiformis*, *Cornus canadensis*. The heath plants as well as mosses are markedly predominant in the subalpine but not in the montane zone.

The successions depend on two primary bare habitats—*rock surfaces* (mainly steep cliffs) and *moraines*, and two secondary ones derived from these respectively—*talus slopes* and *shingle flats*. The rock surface succession was not studied in this region.

A remarkable feature of the *talus succession* is the fact that the pioneers are *trees* and the smaller and lower plants come at a later stage. There are no pre-forest stages except the sparse covering of lichens upon the talus fragments, which is of no consequence in the vegetational development. Two forest stages may be distinguished: the first, dominated by *Betula papyrifera* with occasional willows, the second by the climax conifers. Even these two stages are far from distinct, for certain of the conifers may enter as early and as abundantly as the birches, the only reason why they do not at once attain dominance being that the breaking off of their trunks by falling fragments is always fatal to them. The birch, having met with such a catastrophe, merely replaces its lost shoot with a cluster of stump sprouts, and so is helped rather than harmed by the disaster. The tree seeds germinate in the crevices and cavities among the boulders—obviously the only situation where there is moisture, soil of any kind, and shelter. Possibly the reason why the climax conifers are able to establish themselves so early in so apparently forbidding a habitat is that the shade of the rocks performs the same service for them that the shade of the subclimax trees performs in the normal succession. As the birches become larger and more numerous they lessen the destructive force of the rolling and bounding talus blocks. More and more conifers escape destruction and the forest becomes a mixed conifer-birch aggregation. The elimination of the light-requiring birches and the complete dominance of the climax conifers is now merely a matter of time. The development of the tree contingent may progress at least as far as the mixed birch-conifer condition before any considerable amount of lower growth appears. The establishment of the smaller plants thus awaits and depends upon that of the trees.

The instance of *moraine succession* studied by a comparison of the vegetation of moraines of different ages, began with a mixture of herbs, shrubs, and a few trees—hardly representing a true plant community. The first true community (associates of Clements) is the *Dryas octopetala*—*Arctostaphylos rubra* stage; this is succeeded by the *Salix*—*Betula glandulosa* stage and this again by the climax forest. "Telescoping" however is very marked, since all three stages have their beginnings on the bare moraine and all are still existent on moraines which are passing to climax forest. Thus the reactions of the earlier populations upon the habitat do not furnish the conditions for the appearance of the later. The observed succession would appear rather to depend on differences in the rapidity of development of the different populations, the smallest plants first, then the shrubs, and finally the trees.

The *shingle flats* are formed by the carrying down of morainic material by the torrential streams issuing from the glaciers. The material is roughly sorted through differences in velocity and volume of the flowing water, so that a deposit in a given spot is likely to be rather uniform in size of component materials, and wherever a stream becomes overloaded shingle or silt flats occur. The normal beginning of the shingle flat succession is upon materials wet by surface or superficial underground flow. The pioneers depend on the size of the materials. In true shingle the two most important are annuals—*Epilobium latifolium* and *Saxifraga aizoides*, but a willow appears almost if not quite as soon. In fine silt the first arrivals are more numerous in species and of the sedge or rush type, such as *Carex pauciflora*, *Eriophorum* sp., *Equisetum variegatum*, *Triglochin palustris* and *Juncus* spp. The next stage on wet deposits, whether of fine or coarse material, is a willow thicket made up of several species. *Betula glandulosa* is added and the climax forest follows. If the alluvium is cut into by the stream so as to drain the flat and lower the water table—a thing which happens more rapidly the coarser the material—a xerophytic stage

represented by *Dryas Drummondii* appears, accompanied by *Arctostaphylos uva-ursi* and *Juniperus sibirica*. The willow thicket stage is eliminated and a relatively xerophytic forest stage with *Pinus Murrayana* and *Betula papyrifera* in addition to the climax species such as *Picea Engelmanni* and *Pseudotsuga mucronata* (montane climax). The subalpine shingle flat succession is similar to that on the subalpine moraines but the moraine succession is much more rapid than that upon the shingle flat. The shingle flats close to the glaciers are composed almost entirely of coarse materials, the fine silt having been carried to a greater distance by the streams. The moraines on the other hand are composed of coarse materials embedded in large quantities of fine silt. This character of the moraines is doubtless much more favourable to the rapid development of vegetation.

REVIEW

THE DEVELOPMENT OF VEGETATION

"Plant Succession, an analysis of the development of vegetation," by **F. E. Clements**, Professor of Botany in the University of Minnesota. Carnegie Institution of Washington, 1916. Pp. xiii and 512, with 61 photographic plates and 51 figures in the text.

Professor Clements's large and important work is the first systematic monograph of the phenomena of succession, with a full account of the literature as well as of the author's own researches, that has appeared, and if only for this reason marks an important stage in the progress of synecology. The general lines of treatment follow those laid down in *The Development and Structure of Vegetation* (1904) and *Research Methods in Ecology* (1905), but are considerably developed. Indeed the present volume gives an impression of much greater maturity than the earlier works; and this no doubt is largely due to the very extensive opportunities of studying North American vegetation on the large scale enjoyed by the author in the years 1913-1915, during which period he made numerous journeys through the western half of the subcontinent, from Alberta to Arizona and Texas and from Kansas to California. North America is indeed a region probably unrivalled in the world for obtaining broad views of the great climatic plant communities and their relationships. The West European student of vegetation can get nothing like it at all, both because of the extensive influence of the Atlantic climate, which impresses a wide uniformity on the vegetation over many degrees of latitude and longitude, and because of the old established culture which has replaced, transformed or modified the natural plant communities to such an extent that the reconstruction of original vegetation often presents great difficulties.

Professor Clements's fundamental thesis is that the plant formation is an organism, which shows definite structure in the relation of the plants composing it to one another and to the substratum, and definite functions or processes of which the structure is "the record as well as the result." Furthermore the plant formation can rejuvenate lost parts of itself, can reproduce itself in new situations within the climatic habitat to which it corresponds, and finally has a definite though complex life history or development "comparable in its chief features with the life history of an individual plant." It is this last feature, the life history or development of the formation, which is the subject of the present work.

The plant formation, according to Professor Clements (p. 126), is "the climax community of a natural area in which the essential climatic relations are similar or identical. It is delimited chiefly by development, but this can be traced and analysed only by means of physiognomy, floristic and habitat." This concept indicates a different unit of vegetation from that designated by the term formation in *Research Methods*, where emphasis was laid on the "habitat" characterised by light, humidity and edaphic features such as the water content of the soil. The formations recognised in that work were thus smaller units and included communities now regarded as stages in the development of the formation.

The conception of the formation as a series of developmental stages or successive plant communities arising in a given habitat is originally due to Moss¹, who described the whole of such a series, on a given type of soil, as a "formation" and each well marked stage as an "association," the climax community being called the "chief association." Clements now calls the climax community itself—the adult organism—the formation, while the entire successional series leading up to the climax formation he calls a *sere*. The subordinate units, i.e. the parts of the formation in space, are set out as follows:—

<i>Climax Units.</i>	<i>Seral Units.</i>
Association	Associes
Consociation	Consocies
Society	Socies
Clan	Colony
	Family

The following short definitions of these units may be useful:—

CLIMAX UNITS.

Association. The climax communities associated regionally to constitute the formation are called associations. They agree with their formation in physiognomy and development but differ in floristic and to a certain though unknown degree in habitat. *Examples:* the *Stipa-Agropyrum* prairie, the *Bulbilis-Bouteloua* plains and the *Aristida-Bouteloua* desert plains associations together constituting the prairie-plains climax formation (Note, p. 180): the *Pinus-Abies* association of the *Thuja-Tsuga* Pacific forest formation. This type of community was called a formation by the author in his earlier works.

Consociation. The unit of the association characterised by a single dominant. Consociations approach each other in ecological equivalence and are frequently mixed in various degrees, in which case they are more or less complete expressions of the association². *Examples:* *Bouteloua*-consociation (*Boutelouetum*) and the *Bulbilis*-consociation of the *Bulbilis-Bouteloua* association: *Pinus ponderosa* consociation (*Pinetum ponderosae*) of the *Thuja-Tsuga* association in the Pacific forest. The majority of the communities ordinarily called "associations" come under this head.

Society. A community within an association or consociation characterised by one or more subdominants, i.e. species dominant over portions of the area marked by the dominance of a consociation or an association. Societies are grouped into permanent

¹ Moss, C. E., *Geographical Distribution of Vegetation in Somerset*, 1907.

² Such a mixture is called by the author a *mictium* (p. 129), but it may be suggested that this term would be better restricted, as is indeed proposed on p. 140, to the successional stage where one community is replacing the preceding one in a *sere*, since the mixture of consociation dominants in an association is, as the author remarks, really the association in miniature, and this is an essentially different phenomenon from the transitional mixture of successive *seral* dominants.

and aspect societies: "layer" societies are also distinguished. *Examples: Fragaria*-society in the *Pseudotsuga*-consociation of the montane forest formation (Rocky Mountains)¹; *Lupinus*-society in plains grassland (*Bulbilis-Bouteloua* association).

Clan. An aggregation of a secondary species within an association, consociation or society. A clan is local and restricted in area, but there is no sharp line between a clan and a society. This appears to be the unit generally called a "society" by British ecologists.

SERIAL UNITS.

Associes. This is the developmental equivalent of the association and corresponds with the initial and intermediate "formations" of the author's earlier works and (in part) with the "subordinate associations" of Moss. It differs from the association in being transient, though it may last for many years. It may become an association when the vegetation is held indefinitely in a subclimax stage. *Examples: Scirpus-Typha* associes belonging to the reed-swamp stage of hydrarch succession: *Andropogon-Calamovilfa* associes in development of plains grassland.

Consocies. This corresponds with the consociation in the same way that associes corresponds with association. *Examples: Aspen (Populus tremuloides)* consocies in the development of the montane climax conifer forest (Rocky Mountains): Sand-reed (*Calamovilfa*) consocies in the development of plains grassland.

Socies. This is the developmental equivalent of the climax society.

Colony. "The colony is an initial community of two or more species. It is practically always the direct consequence of invasion, and hence is characteristic of the early seral development in bare areas." "Colonies resemble clans in their usually limited size and in the absence of a clear relation to the habitat, because they are still in the process of invasion."

Family. "A group of individuals belonging to one species. It often springs from a single parent plant, but this is not necessarily the case any more than in a human family.... Families are usually small since they are more readily invaded when large, and consequently pass into colonies. They are especially typical of bare areas and initial stages."

The system of vegetation units just described is logically complete, corresponds well with the actual phenomena of unmodified vegetation and has the great theoretical merit of resting upon development as a basis. As the author admits, only those ecologists actually interested in the development of vegetation are likely to use the seral units. For others the one set of units will suffice, without regard to the distinction between development and climax.

In his discussion of the process of succession itself the author brings out the fairly well-known principle that it consists essentially of a series of reactions of successive plant populations upon the habitat, each reaction rendering the habitat less favourable for the existing population and favouring its replacement by the next. The period during which each population holds the ground depends upon the degree of dominance which it exerts. "Effective dominance can only occur when the prevailing life-form exerts a significant reaction which holds the population in a certain stage until the reaction becomes distinctly unfavourable to it, or until the invasion in force of a superior life-form. Dominance is

¹ This is a case of a ground society in a layered community and must be distinguished from the type of a society in the tallest layer of the association or consociation. It is not clear why the author should hold (p. 130) that "in forest, societies are formed only beneath the primary layer of trees." There seems to be confusion here between two meanings of the term sub-dominant.

then the ability of the characteristic life-form to produce a reaction sufficient to control the community for a period....Each stage is a minor process of stabilisation, a miniature of the increasing stabilisation of the sere itself." The climax "is reached when the occupation and reaction of a dominant are such as to exclude the invasion of another dominant."

This is a clear account of the probably normal course of primary succession, but we scarcely think that the author lays enough stress on the deviations which actually occur—the far-reaching "telescoping" of phases, the appearance of plants or populations out of their "proper" order and so on. These phenomena are, it is true, mentioned, but it seems probable that they are far commoner than the reader would suppose. Until a great many more successions have been thoroughly studied, it is unwise to lay too much stress on generalised statements. In regard to the rôle of the reactions of populations on the habitat in preparing the way for new populations we must also beware of rigid generalisation. The reader may consult with advantage Mr W. S. Cooper's account (see p. 196 of the present number of this *Journal*) of succession at Mount Robson, British Columbia. On the talus of the subalpine zone trees arise at once without any preparation by lower plants, and in the moraine succession the establishment of herb and shrub populations before the tree population depends upon the shorter time taken by the former to develop, not upon the reactions of the former upon the habitat preparing the way for the latter, since all three populations are shown to start their development about the same time.

In terrestrial regions with a "mesophytic" climate the climax is forest. In dry regions, in very cold regions and in regions where the soil has peculiar characters the climaxes are different. Where such a factor as "climatic" water-supply changes regularly as we proceed across a continent, as is the case from the eastern states of North America to the foot of the Rocky Mountains, the climax formations are regularly zoned in correspondence. This climatic zonation of climaxes would appear to be, and is usually taken as, essentially distinct from the type of zonation occurring for instance round ponds and marshes, where the zones are the expression of successive seral communities each of which will ultimately give place to the climax. Professor Clements however holds that there is no essential difference between these two kinds of zonation. The climax of each climatic zone is the potential climax of the next in either direction if the climate swings in the corresponding way. In the case for instance of the advance or recession of an ice-sheet the zone occupied by a given climax at a certain stage of the recession or advance will be occupied by successively higher climaxes in the first case and by successively lower ones in the second. The records preserved in peat bear witness to such a succession of climaxes. The author also points out the identity in certain cases of the subfinal stage of a sere with the climax stage in an adjacent climatic region; for instance *Pinus ponderosa* forms a xerophytic climax in one of the lower altitudinal zones of the Rocky Mountains, while 2000 to 3000 feet higher it is the subfinal stage in the development of spruce forest. Such cases, however, do not appear to the reviewer to be "conclusive proof of the developmental connexion" of climax zones, but rather of parallelism between succession and climatic zonation. If for instance the conditions become progressively more mesophytic in passing through the stages of a sere, there may well be a parallel or even an identical population as between a subfinal stage and the climax of an adjacent drier region. But the correspondence is not exact nor universal: for instance there is no "plains grassland" stage in the Rocky Mountains succession. And so in many other cases. The correspondence is an incomplete parallelism, not an essential identity.

Professor Clements criticises adversely the whole conception of "retrogression" in succession. He denies that there is such a thing as retrogressive succession, and points out that what is called by that name is in reality due to the destruction of a climax or

some earlier stage and the consequent establishment of an earlier stage of the progressive succession, which resumes its normal course unless the destructive cause again intervenes. The most widespread case of this process is the destruction of forest by fire or grazing or both combined, resulting in the establishment of scrub or grassland, which will again progress to forest if the fires cease and the grazing is withdrawn, unless indeed the destruction has been so widespread as to result in the absence of seed to provide for the rejuvenation of the forest. In the last case, or if the fires are recurrent or the grazing permanent, the vegetation remains in the subclimax stage determined by these factors.

The same thing is true in "dynamic" regions where natural agencies, such as flooding, blowing sand, erosion by mountain torrents, avalanches, talus formation, and the like, maintain the succession in a subclimax stage, which varies according to their nature and the frequency of their incidence. The author will have nothing to do with a classification of formations such as Crampton's¹ which makes a primary division into "stable" and "migratory" formations, the latter characteristic of the constantly shifting vegetation of dynamic or "geologically active" areas. For Clements all this shifting vegetation is simply composed of early stages of seres which would ultimately lead to a stable climax type if the physiographic agents would let them alone. On the same ground he refuses to regard as fundamental Cowles's classification of plant successions according to the climatic, topographic or biotic factors which control the successions, holding that all formations and the seres leading up to them are controlled by climate, that the *causes* of the initiation of seres may be topographic (physiographic) or biotic, while the causes of the actual advance of the sere are the biotic reactions of successive plant populations on the habitat.

It is interesting to try to apply Professor Clements's system of concepts to the vegetation of the British Isles. The deciduous forest of north-western Europe, quite parallel as it is with that of the eastern United States, would be the first formation we should have to recognise. In this we should distinguish a beech-consociation, an oak-consociation, and an ash-consociation, each determined by edaphic habitats². Various mixtures of the dominants more completely represented in the mixed deciduous forests of the continent would represent one or more associations. Birch and pine in the south of England would probably represent consocieties and an associates leading up to the climax, but forming a fairly stable subclimax on certain light soils. In the hydrosere alder and willow would represent an associates; and alder, willow, ash and birch different consocieties leading probably to an oak climax as the soil becomes drier.

Zoned to the north of the deciduous forest formation we should recognise a birch-conifer formation represented to-day by the few fragments of pine forest (a pine-consociation) still remaining in Scotland. The much more extensive birchwoods of Scotland and of the altitudinal zone above the oakwoods of the north of England would probably represent a distinct consociation of this formation. The frequent mixture of the two would be the single association of this formation.

The great semi-natural grassland communities of the British Isles are probably mainly due to forest destruction and grazing. They may be regarded as modified subclimaxes in Clements's sense; but it is very unlikely that in anything like their present form they are in the direct line of the original primary forest successions. The widespread destruction of forest is doubtless an important factor in preventing a return to forest, owing to the removal of seed parents and the consequent absence of the seed necessary for rejuvenation.

¹ Crampton, C. B., "The Geological Relations of Stable and Migratory Plant-formations," *Scottish Botanical Review*, 1912.

² The edaphic differences in the habitats and in the floristic of these consociations in the British Isles are much more strongly marked than is contemplated, apparently, by Prof. Clements.

It is difficult to say how far the competition of the established grasses or the difficulties which the presence of a continuous grass carpet opposes to the germination and establishment of tree seedlings, may be factors in preventing the return of forest. Experiment alone can decide this question. Some of the chalk down grassland has very probably never borne forest owing to the dryness of soil consequent on the lowness of the water table, though forest destruction and grazing have no doubt greatly extended the chalk grassland area. "Primitive" chalk grassland would be an edaphic extension northwards of a continental grass community, modified by sheep grazing.

Of heath the same thing may be said. Most of our heaths—perhaps all—are probably due to forest destruction, and may be regarded with Clements as a quasi-permanent subclimax stage in forest succession. Clements admits the formation of "ortstein" and hard pan as a secondary condition checking the development of forest, but the surface conditions obtaining on certain heaths have a similar effect, and apparently maintain the heath indefinitely apart from grazing or burning. Again experiments are wanted to clear up this question.

In the case of moor Clements admits that the invasion of *Sphagnum* is a real cause destroying or preventing the development of forest. He attributes this to the water the *Sphagnum* holds and consequently regards the invasion as comparable with destruction or prevention of development by flooding. But this point of view does not apply to the extensive upland moors of north Britain in which *Sphagnum* plays quite a minor rôle, and which are determined by a combination of climatic and edaphic conditions over wide areas. And such moors can by no stretch of language be described as a subclimax stage in the development of forest.

From a consideration of these cases the practical drawbacks to Professor Clements's restriction of the concept of formation to a *climax stage determined by climate* become apparent. Granted that this concept furnishes the most satisfactory scheme of classification for the great forest climaxes of the world, it leaves out of account the establishment of *permanent* communities of distinct life-form owing to edaphic conditions or to conditions determined by biotic reaction on the soil. It was to cover cases of this kind that Schimper introduced the term *edaphic formation*, and if its use be not allowed it is difficult to see how we are to classify such communities. Perhaps Professor Clements would regard our northern moors as constituting an intermediate altitudinal or latitudinal formation between forest and alpine formations on the one hand or between forest and tundra on the other, for it is true that though largely determined by edaphic conditions the upland moors are characteristic of a certain type of climate. In any case, if Clements's concept of formation be accepted it is clear that the determination of the actual formations existing in any region, and to a less extent of the other units of the system as well, becomes difficult and doubtful, since it will be dependent on the elucidation of successional phenomena which are often exceedingly hard to establish, especially in regions where the vegetation has been modified artificially to a large and unknown extent. This fact will tend to militate against the general adoption of the concepts. At the same time there can be no doubt that the attempt to apply so clear and logical a system to actual vegetation will have a very beneficial effect. The difficulty inherent in the system adopted in *Types of British Vegetation*, for instance, of obtaining agreement as to what really constitutes "fundamental identity of habitat" is avoided, and the emphasis is laid on the vegetation itself as determined by its actual development.

A very useful feature of the work under review is the very complete set of abstracts of publications dealing with succession, not only in North America but in the rest of the world, and the careful and full discussion of the views of such authors as Cowles and Moss on the succession and on vegetation units.

The book closes with a long section devoted to the phenomena of the succession of vegetation in past times as revealed by the geological record. This certainly constitutes a bold attempt to apply the author's principles to the past history of vegetation. Of its value in detail it is impossible to speak without a far greater knowledge of fossil floras than the reviewer can claim.

The new terminology adopted by the author, like his system of concepts, is very complete. It is certain that the majority of readers will find it much too complete! In the absence of a glossary it is difficult to say how many new words are introduced, but a very great many, far more than the average worker—who takes to new terms slowly and only under pressure of absolute necessity—will be likely to adopt. Of some at least it may fairly be said that they are not necessary because the phenomena to which they relate will be referred to but seldom. The new terms are however all compact and apt—a consequence of the author's quickness of mind and of his extensive knowledge of Greek roots and their linguistic use. A few will probably come into general use fairly soon.

The photographs of vegetation are of great and uniform excellence, both in choice of subject to illustrate the text, in technical quality and in reproduction.

Plant Succession is a very notable and a very valuable contribution to the subject, and its author may be warmly congratulated on its production.

A. G. T.

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VOLUME V

WITH TWENTY PLATES AND NUMEROUS FIGURES
IN THE TEXT



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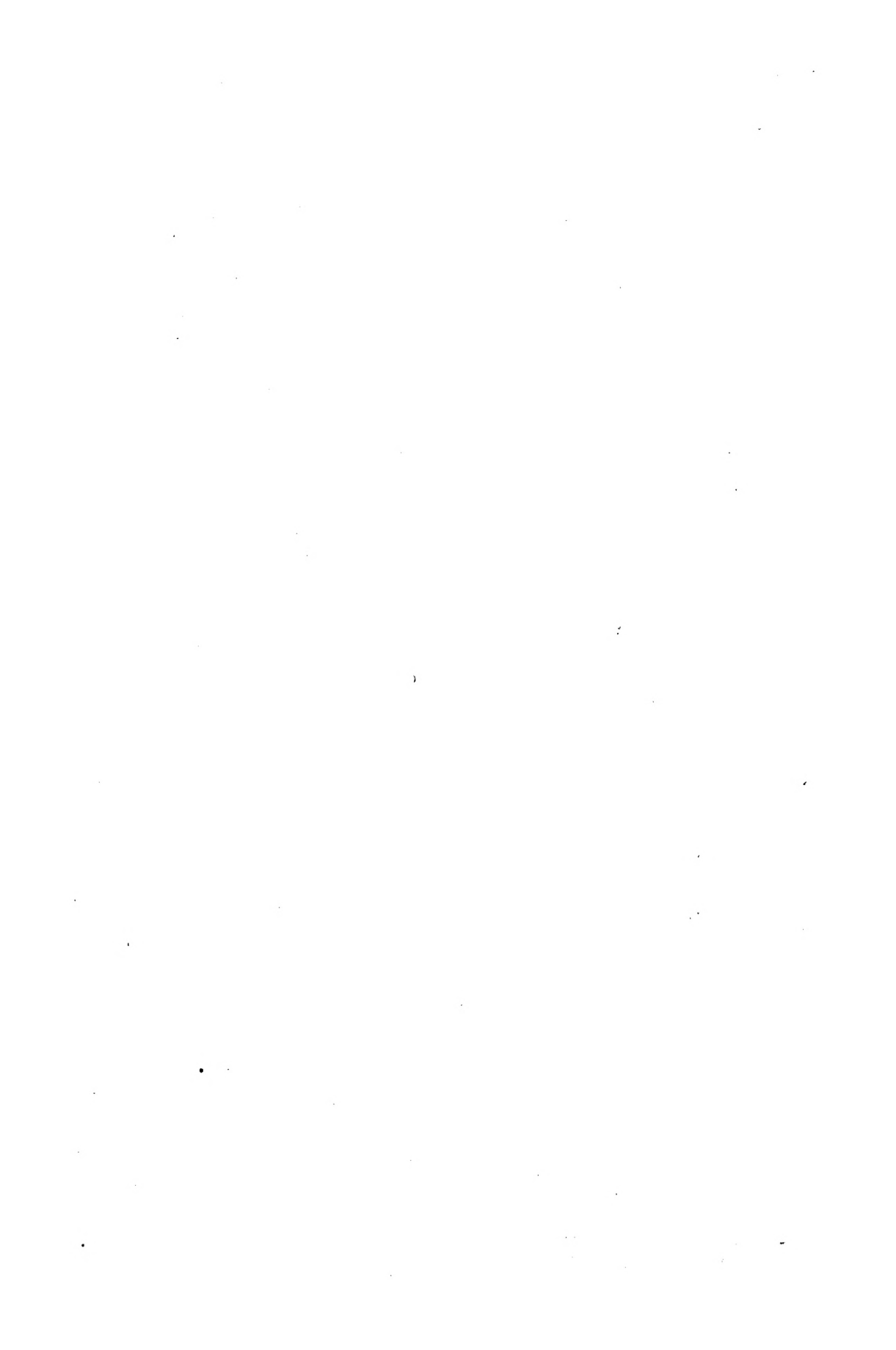
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ON THE ECOLOGY OF THE VEGETATION OF BRECKLAND.

III. GENERAL EFFECTS OF RABBITS ON THE VEGETATION¹.

BY E. PICKWORTH FARROW

(With Plates I—VI and one Figure in the Text)

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It was shown in Part II that rabbits produce so great an effect upon the vegetation of Cavenham Heath and other heaths of Breckland as to cause the main *Calluna* heath associations to degenerate to grass-heath and to determine the relative distributions of these two main associations². It therefore seemed advisable to devote considerable attention to any other effects which rabbits might have upon the vegetation. It is known that rabbits exert a very great effect upon vegetation elsewhere in the country, and as a single instance the influence of rabbits on the vegetation of Blakeney Point in Norfolk may be cited³.

¹ Part of a Thesis accepted for the degree of Doctor of Science in the University of London.

² Farrow, E. P. "Factors Relating to the Relative Distributions of *Calluna* heath and grass-heath in Breckland." This JOURNAL, 4, No. 2, pp. 57—64.

³ Oliver, F. W. "Some Remarks on Blakeney Point, Norfolk." This JOURNAL, 1, No. 1, pp. 14 and 15.

RABBIT-PROOF FENCES.

In order to see what other effects rabbits might have upon the vegetation, the rabbit-proof fence which runs across the southern end of Cavenham Heath was first examined. This southern fence runs from the point marked 14 to the point marked 15 on the map already given¹. It was erected 14 years ago. There is a sharp change in the character of the vegetation between the two sides of this fence (see Pl. I, Photos. 1 and 2). The difference chiefly manifests itself in the much greater height and luxuriance of the vegetation and in the far greater number of inflorescences on the protected side of the fence. On the unprotected side there are practically no inflorescences and much bare sand is exposed (see Photo. 1).

The area on the protected side of the fence is also far richer floristically than the larger unprotected area of Cavenham Heath, containing many plants which are not found at all on the main portion of the heath, which is subject to rabbit-attack. The following are some of the chief plants which occur on the protected side of the rabbit-proof fence whilst they are either rare or absent on the unprotected side: *Convolvulus arvensis*, *Silene inflata*, *Lychnis alba*, *Ornithogalum umbellatum*, *Lotus corniculatus*, *Geranium molle*, *Crepis capillaris*, and *Achillea millefolium*. Their absence on the unprotected side is probably chiefly due to the far greater amount of rabbit-attack in that position.

A comparison of Photos. 1 and 2 shows that there is a greater difference in the vegetation on the two sides of the fence in Photo. 2 than in Photo. 1. On the protected side of the fence in the region shown in Photo. 2, *Carex arenaria*, *Urtica dioica* and *Agrostis vulgaris* are growing fairly luxuriantly—much more so than the vegetation on the protected side in Photo. 1. This is probably chiefly because the region shown in Photo. 2 is at a lower level and in consequence not so dry as that shown in Photo. 1; so that water supply is probably not so severe a limiting factor to the growth of the vegetation. Although the protected vegetation can thus grow taller in this region yet the vegetation on the rabbit-attacked side of the fence is eaten nearly as close as that shown in Photo. 1, the heavy rabbit-attack keeping it down nearly to the same low level in both cases. Nevertheless the rabbit-attacked vegetation in Photo. 2 forms a somewhat closer turf than that in Photo. 1 and not so much bare sand is exposed.

In the region shown in Photo. 2 it should be noted that *Carex arenaria* is largely dominant on the protected side of the fence, and is absent on the rabbit-attacked side. The heavy rabbit-pressure in this region is sufficient to prevent this plant from effectually invading the rabbit-attacked area by rhizome growth through the fence and thus eventually smothering the grass vegetation.

¹ This JOURNAL, 8, No. 4, p. 217.

Carex arenaria is also present on the protected side of the rabbit-proof fence on the western side of the heath and is absent on the rabbit-attacked side. The same state of things also occurs in various other localities in Breckland.

RABBIT-PROOF CAGE ON THE RELATIVELY PROTECTED SIDE
OF THE RABBIT-PROOF FENCE.

A few rabbits occur on the relatively protected side of the rabbit-proof fence seen in Pl. I, Photos. 1 and 2. In order to determine the effect of this small number of rabbits on the vegetation, a rabbit-proof cage was erected on the protected side of the fence¹.

For some time there was only a small difference between the vegetation inside and outside the cage, but *Galium verum*, *Crepis capillaris* and *Sedum acre* grew and flowered appreciably better relatively to the grasses inside than outside the cage (see Pl. II, Photos. 3 and 4), showing that these plants suffered more than the grasses from the relatively few rabbits present on this side of the fence. After a period of three years the difference between the vegetation inside and outside the cage became much more marked, showing that the attack of even a few rabbits may have a considerable cumulative effect on the vegetation. *Rumex acetosella*, *Sedum acre*, *Galium verum*, *Crepis capillaris*, *Carex arenaria*, *Agrostis vulgaris*, *Festuca ovina* and *Holcus lanatus* eventually grew and flowered much better inside the cage than outside. Inflorescences of the four first named plants were either non-existent or very rare outside the cage although they occurred freely inside (see Pl. II, Photos. 3 and 4). It was very apparent that on the whole plants with tall vertical shoots and inflorescences eventually suffer more from increasing rabbit-attack than plants with shoots which can grow very close down to the surface of the soil. Probably vertically growing and tall shoots and inflorescences attract the attention of the rabbits, and are easier for them to cut off than more dwarf growing plants. Such plants in grassland are also usually fewer in individuals per unit area than the grasses and are thus more readily exterminated.

Sometimes ephemerals grow and flower when exposed to fairly heavy rabbit-attack and at first sight these might appear to be exceptions to the generalisation that vertically growing shoots and inflorescences suffer especially heavily from rabbit-attack; but the explanation in these cases probably is that though the ephemerals are as a whole heavily attacked by rabbits, their

¹ By means of rabbit-proof cages the rabbit factor can be entirely removed from the environment and its separate effect studied, if allowance is made for time. It is rarely that we can thus completely isolate an ecological factor in order to study its special effects. Wire netting of one inch mesh should be used, since it is possible that very small rabbits can squeeze through $1\frac{1}{2}$ inch meshes. Wire netting of heavy gauge should be used for the sake of durability.

short annual period of vegetation exposes them to attack for a considerably less period than is the case with most other plants and that thus some of them manage to survive the rabbit-attack and are able to flower.

RABBIT-PROOF CAGE ON THE RABBIT-ATTACKED GRASS-HEATH ASSOCIATION.

Another rabbit-proof cage (see Pl. III, Photos. 5 and 6) was fitted up on the unprotected side of the rabbit-proof fence in the middle of the degenerate grass-heath association on Cavenham Heath, about half way between the point marked 13 on the map and the present degenerating edge of the *Calluna* heath. The rabbit-attack in the region where this second cage was erected is extremely heavy. The portion of the degenerate grass-heath which was enclosed inside this second rabbit-proof cage quickly began to go back to *Calluna* heath as can be well seen in Pl. III, Photos. 5 and 6. It has already been shown¹ that the *Calluna* roots remain alive in the soil for some time after all the upper portions of the *Calluna* plants have been killed by rabbit-attack and decayed by the damp luxuriant growth of *Cladonia*; and that the still living *Calluna* roots endeavour to send up fresh stems which are however normally quickly eaten off by the rabbits until the roots eventually die. Inside this cage, however, the young *Calluna* shoots produced by the still living roots are protected from rabbit-attack, and they have already grown to a height of 20 cms. and borne many flowers. (See Pl. III, Photo. 6. Note the great contrast between the vigorous and flowering young *Calluna* shoots inside the cage and the closely nibbled down shoots of *Calluna* outside on the right of the photograph.)

Thus it will be seen that the area of degenerate grass-heath enclosed inside this cage is quickly reverting to *Calluna* heath now that the heavy rabbit "pressure" on the enclosed area is removed.

Agrostis vulgaris and *Rumex acetosella* are also growing much better inside this cage than outside and are flowering fairly profusely, whilst outside no inflorescences of these plants can be found, all of them being eaten down by the rabbits. Possibly however one of the most interesting things about this cage is that each summer since it was erected it has contained a number of *Campanula rotundifolia* flowers (see Pl. III, Photos. 5 and 6) although no other harebell flowers occur on the grass-heath outside this cage for a great distance all around, in spite of the fact that the plant itself is present. This is a striking additional instance of the especially injurious effects of rabbits upon inflorescences. These instances make it appear highly probable that the presence of rabbits severely checks the reproduction of many plants by seeds.

¹ "Factors Relating to the Relative Distributions of *Calluna* heath and grass-heath in Breckland." This JOURNAL, 4, No. 2, p. 61.

This particular detrimental influence may well appreciably affect the flora of many regions in England and other countries where rabbits are numerous and ubiquitous.

EFFECTS OF RABBITS ON THE *CAREX ARENARIA* ASSOCIATIONS.

In addition to attacking the *Calluna* heaths and grass-heath areas rabbits frequently attack the dense *Carex arenaria* associations which are so common in parts of Breckland. Rabbits also attack *Carex arenaria* at Blakeney¹.

When the *Carex arenaria* associations in Breckland are competing with grass-heath (degenerated *Calluna* heath) the *Carex* associations are usually badly attacked by rabbits on their external edges, but when the *Carex* associations are competing with *Calluna* the external edges of the *Carex* associations are not usually much attacked by the rabbits. The probable chief cause of this difference in the rabbit-attack on the external edges, as opposed to internal edges, of the *Carex* associations under these two different conditions are dealt with in detail later on (see pp. 10—16).

Areas bare of *Carex* and often occupied by the typical degenerate grass-heath association and sometimes with decaying fragments of *Calluna* frequently occur around collections of rabbit burrows in the large dense *Carex arenaria* associations (see Photo. 6 in Part I)². The *Carex* shoots around these bare areas are always badly eaten by the rabbits.

Many of these large areas of *Carex arenaria* in Breckland were probably fairly recently typical *Calluna* heaths which have completely degenerated owing to rabbit-attack, and have now become replaced by pure *Carex arenaria* associations, except just around the rabbit burrows where the rabbits, after having caused the *Calluna* heath to degenerate, now keep back from their burrows the otherwise spreading *Carex* (cf. the absence of *Carex* on the rabbit-attacked side of the fence seen in Pl. I, Photo. 2). It was the frequent presence of the typical degenerate heath flora along with decaying remains of *Calluna* around rabbit burrows where the dense *Carex arenaria* is now kept back by the rabbits, that first suggested the probability that many of the *Carex* areas were fairly recently typical *Calluna* heaths.

It has already been stated that *Carex arenaria* very likely became established in this now inland district in ancient post-glacial times when the original bay of the Wash extended near to the western border of the district. The *Carex* has thus probably been in the district from ancient times, and could not have continually spread at its present rate or it would be all over the district by now. The probable explanation of the recent rapid spread of *Carex arenaria* in Breckland is that it is due to the presence of rabbits in the district. Rabbits have only been introduced into England since the

¹ Rowan, W. "Note on the Food Plants of Rabbits on Blakeney Point, Norfolk." This JOURNAL, 1, No. 4, p. 274.

² This JOURNAL, 3, No. 4, Plate XVIII.

Neolithic epoch, and in many instances they have only been preserved from their natural enemies during the last few decades or more recently still. Though they attack *Carex arenaria* they apparently only eat it as a matter of necessity, while they eat *Calluna vulgaris* much more readily. Thus it comes about that, in a zone where *Carex* and *Calluna* are competing, rabbits confer a great relative advantage upon the *Carex* and enable it to spread, owing to the fact that, although they eat it severely, they eat its competitor to a greater extent. This differential action of rabbits upon competing plants has already been mentioned in connection with the degeneration of *Calluna* heath to rabbit-attacked grass-heath¹. It is a striking fact that rabbits should be able to confer such very great relative advantages upon certain species within a given sphere of competition even although they may eat these species very severely.

EFFECTS OF RABBITS UPON THE *PTERIS AQUILINA* ASSOCIATIONS.

The rabbits often also attack some of the fronds of the dense *Pteris* associations which are common in Breckland. They do not appear to like the bracken fronds, which are apparently only attacked when the rabbits are very short of food, or when the alternative food supply consists of some very unattractive plant such as *Erica tetralix*. Only the fronds on the extreme edges of the bracken associations are attacked. The rabbits usually only nibble the softer parenchymatous parts of the frond stalk so that the upper part of the frond topples over, and this usually remains connected with the lower portion of the stalk until the exposed sclerenchyma decays sufficiently for the wind to blow the collapsed upper portion away. Apparently the rabbits only taste the frond stalks, since they usually do not eat them at all extensively even when hard pressed for food. It is very apparent that owing to some cause or other—possibly bitterness or toughness—bracken is not a suitable food for rabbits.

Sometimes, however, when a great depth and area of degenerate grass-heath, associated with many rabbit burrows and innumerable rabbits anxious for extra food, borders upon a bracken association, the total temptation of the rabbits to test the bracken stalks for food is sufficiently great to cause considerable depths of bracken on the edge of the association to degenerate. This has occurred on Cavenham Heath near the spot marked 2 on the map, where the rabbit-attack is extremely heavy.

Usually however the rabbits do not attack the bracken at all extensively, and as the edge of a bracken association advances by rhizome growth, the rabbits which have their burrows on the ground which has recently become occupied by the spreading bracken and which formerly lived on the more

¹ **Farrow, E. F.** "Factors Relating to the Relative Distributions of *Calluna* heath and Grass heath in Breckland." This JOURNAL, 4, No. 2, p. 64.

attractive vegetation previously occupying the ground are driven to go for their food to the more attractive vegetation on the zone immediately outside the advancing edge of the bracken. The result of this is that if, for instance, the bracken is advancing over *Calluna*, there is usually a bare zone, or a zone of *Calluna* degenerating rapidly owing to attack by rabbits coming from the ground recently occupied by the *Pteris*, just in front of the advancing edge of the *Pteris* association. Thus, especially in the cases of large *Pteris* associations which have already covered a large rabbit-occupied area, the advancing edge of the *Pteris* does not have to compete with the *Calluna* which formerly occupied the ground, and for this reason the bracken can advance much more rapidly than if it had had to compete with the original heather. The driven out rabbits eat the heather and thus tend to prepare the way for the advancing bracken. Thus the rabbits through attacking its competitors and scarcely attacking the *Pteris* at all confer a great advantage upon the bracken, which is thereby enabled to spread very rapidly—far more rapidly than it could otherwise do.

When bracken is competing with *Carex*, the presence of rabbits also confers a relative advantage upon the bracken by inflicting a differential rate of injury upon its competitor (as already described) owing to the fact that the rabbits attack the *Carex* more than the bracken; but in this case the advantage conferred on the bracken by rabbits is not nearly so great as where bracken is competing with *Calluna*, since the attack on the *Carex* relatively to bracken is not nearly so great as the attack on the heather relatively to bracken. It is hoped to measure accurately (by means of quadrats and orientated photographs) the relative rates of advance of bracken over *Calluna* and over *Carex* in the presence of rabbits and in the absence of rabbits respectively.

EFFECTS OF RABBITS UPON *JUNCUS* SPP., *SALIX REPENS* AND *ERICA TETRALIX*.

The rabbits also attack various species of *Juncus* on Cavenham Heath (chiefly *Juncus conglomeratus*, *J. obtusiflorus* and *J. supinus*). In some places *Juncus* is attacked very heavily. Often when the *Juncus* borders upon open water the rabbits can only reach the plants on the drier edge of the *Juncus* zone and the plants within reach of the rabbits are usually badly eaten down, all their inflorescences being eaten off, so that they are entirely prevented from flowering, while the plants growing where the water is deeper and thus out of reach of the rabbits produce inflorescences freely.

Sometimes the rabbits also attack young stems of *Salix repens*. They usually only do this however where their alternative food supply is very unattractive.

Erica tetralix is another plant which is not usually much attacked by rabbits at Cavenham. Apparently the rabbits do not like it—possibly this

may be largely due to the hairy nature of the plant. *Erica tetralix* is, however, eaten less reluctantly than bracken. The *Erica*, like *Carex*, *Pteris* and *Salix repens*, is eaten chiefly in places where there is no alternative source of food supply, or where the alternative sources of food supply are about as unattractive as these plants are themselves.

Erica, *Carex*, *Pteris* and *Salix*, all rabbit-attacked under these latter conditions, can be well seen in Photo. 2, Part I¹. In this instance, the rabbit-attacked *Erica* plants are surrounded, on one side by unattractive *Pteris* and on the other side by unattractive *Salix repens*. Under these special conditions, where the rabbits only have a choice of evils for their food supply, all these very unattractive plants are appreciably rabbit-attacked as can be seen in the photograph, and the *Erica tetralix* bushes have even taken on the particular rounded shape without projecting shoots characteristic of rabbit-attacked bushes. Since the rabbits do not eat *Erica tetralix* nearly so readily as they attack *Calluna vulgaris*, they confer a great advantage upon the *Erica* and enormously increase its possible distribution in a zone where it is competing with *Calluna vulgaris*, in spite of the fact that they eat it.

This increase in the distribution of *Erica* relatively to *Calluna* and the resulting raising of the *Erica* zone in a *Calluna* heath owing to the differential action of rabbits upon these two competitors has probably a bearing upon the occasional occurrence of *Erica tetralix* in certain very slight depressions on Cavenham Heath only slightly less dry than the surrounding *Calluna* heath itself, as well as in the much damper hollows. For if the distribution of the *Erica* relatively to the *Calluna* has been greatly favoured by the differential action of the rabbits and the *Erica* zone has thus been raised, the successful competition of the *Erica* with the *Calluna* in those places which are only slightly less dry than main *Calluna* heaths themselves may possibly be partly explained.

EFFECTS OF RABBITS UPON *SOLANUM NIGRUM*, *CONIUM MACULATUM*, *URTICA DIOICA* AND *U. URENS*.

Solanum nigrum, *Conium maculatum*, *Urtica dioica* and *U. urens* are the only herbaceous plants which have been found on Cavenham Heath which are not attacked by rabbits more or less severely in one place or another. It has already been indicated that the heavy rabbit-attack by destroying their competitors and practically not eating these poisonous and stinging plants at all must confer a very great advantage indeed upon them. It is very striking to see for instance a herbaceous *Solanum nigrum* plant green and growing vigorously although it is surrounded on all sides by brown, dead and decaying rabbit-attacked *Calluna* and loose *Cladonia*.

¹ "General Description of Breckland." This JOURNAL, 3, No. 4, Pl. XVIII.

EFFECTS OF RABBITS ON SEEDLING TREES RESULTING IN CONFINING
TREE GROWTH TO THE VALLEYS.

It has already been stated that various artificial plantations of birch and introduced pines have been made upon the upper portions of many of the Breckland heaths—upon Cavenham Heath for instance—although previously there were no tree plantations in the district. Seeds from some of these plantations have apparently been able to colonise some of the minor valleys. In many of these cases (see Photo. 1, Part I)¹ there were very few trees in the valleys 50 years ago, but these have apparently produced much seed and they are colonising the surrounding region with many young trees.

In practically all cases the bases of the stems of these young trees are very badly attacked by rabbits (see Pl. IV, Photos. 7 and 8) and in most instances the young trees die from this rabbit-attack. Though practically all the young trees in the valleys are badly attacked by rabbits, and though most of them succumb to the attack, yet some of them do manage to struggle on and survive it, and when they reach a certain height—apparently about 3 feet in the case of *Pinus sylvestris* on Cavenham Heath—their stems become relatively immune to the more serious effects of the rabbit-attack and the trees can then grow with comparative ease.

By far the greater proportion of those young trees which do manage to survive the rabbit-attack to which all of them are subjected, are those situated near the bottoms of the valleys; and as one passes up the sides of the valleys, a greater and greater proportion of the young trees succumb to rabbit-attack, until near the upper edges of the valleys all the young trees eventually succumb before they can reach a size when they would become immune. The rabbit-pressure, as indicated by the number of rabbit dung pellets per unit area, is approximately constant all over the sides of the valleys, and the survival of the young trees on the lower portions of the valley sides is not due to a diminished intensity of rabbit-attack in these zones.

It appears probable that the true explanation is that near the bottoms of the valleys, where there is a much greater available water supply, the young trees can just produce fresh tissue faster than the rabbits eat it and can often just repair the damage caused by the rabbit-attack and survive it. Thus they just manage to grow and struggle on until they reach a size when they become relatively immune and can grow comparatively easily. On the sides of the valleys where the water supply is much less, the growth of the young trees is retarded and they cannot produce fresh tissue as quickly as the rabbits eat it. Thus they are killed by the rabbit-attack before they can reach a sufficient size to become immune.

A portion of the upper area of Cavenham Heath (marked 16 on the map) near the Icklingham road has been fenced off from rabbit-attack and little

¹ "General Description of Breckland." This JOURNAL, 3, No. 4, Pl. XVIII.

pine trees are growing inside this rabbit-proof enclosure on the dry upper portion of the heath. In this locality the young pine trees can only grow slowly even when protected from rabbits, yet nevertheless they can grow if protected even on this dry upper portion of the heath, while outside the rabbit-proof enclosure on the dry upper areas, pine seedlings are always killed by the rabbits before they can attain any size.

It is thus seen that the rabbits prevent the dry upper areas of Breckland from being colonised by young pines and from being ultimately converted into fairly useful pinewoods. Such pinewoods would probably be of far more value to this island country than are the rabbits. If it had not been for the largely incidental suppression of the natural enemies of the rabbits consequent upon pheasant preserving, a considerably larger area of Breckland would probably now have been converted into spontaneous pinewoods.

The limitation of tree growth to the damper valley bottoms and sides consequent upon biotic attack on the seedlings, whereas if it were not for this the tree growth would spread all over the drier upper areas, is an extremely interesting biological phenomenon which probably has a great bearing upon the zonation and distribution of natural vegetation in many parts of the world—for instance in parts of Australia. In this connection it is interesting to note that tree growth on the prehistoric steppes of Continental Europe was apparently largely confined to the valley sides¹. Many herbivorous animals were present on these prehistoric steppes, and it seems very possible that the limitation of the tree growth to the valley sides was largely due to the action of biotic attack upon the seedlings, as happens in Breckland at the present day. It is clear that the factor of biotic attack, in addition to the water factor, must be taken into account in considering such cases.

ZONATION OF VEGETATION AROUND RABBIT BURROWS IN BRECKLAND.

It has already been mentioned that areas bare of *Carex* often occur around collections of rabbit burrows in the dense and extensive *Carex arenaria* associations in Breckland (see page 5 and also Pl. XIX, Photo. 6 in Part I). Some instances were observed, however, on Tuddenham Heath, in which *Carex arenaria* is associated with collections of rabbit burrows in *Calluna* heath whilst it is absent elsewhere (see Pl. V, Photo. 9). These cases are very interesting because this distribution of *Carex* in relation to the collections of rabbit burrows is quite opposite to the apparently more usual cases in which the *Carex* is absent around the collections of burrows whilst it is present elsewhere. In order to obtain information with a view to determining the causes of this reversed distribution of the *Carex* in the two classes of cases the transition zone between the *Carex* association, where it is present immediately around

¹ Geikie, J. "The Tundras and Steppes of Prehistoric Europe." *Scottish Geographical Magazine*, 1898.

the burrows, and the surrounding *Calluna* heath was first examined (see Pl. V, Photo. 10). In passing from the *Carex* zone to the *Callunetum* the *Carex arenaria* shoots and leaves gradually become shorter, weaker and fewer in number, and occur chiefly along the numerous rabbit tracks (see Pl. V, Photo. 10). On the other hand, the *Calluna* bushes gradually become more numerous and of greater height until the typical *Calluna* heath association itself is reached (see Pl. V, Photo. 10). The *Calluna* bushes of the transition zone tend to have the rounded form, with no projecting shoots, characteristic of rabbit-attacked bushes. The transition zone is, in fact, a narrow but otherwise typical zone of *Calluna* heath degenerating through rabbit-attack, with the addition that a generating zone of *Carex arenaria* is associated with it, and with the exception that, in these special cases, a luxuriant growth of *Cladonia* has not up to the present been found associated with the degenerating *Calluna*. Possibly this may be largely owing to the presence of the generating zones of *Carex arenaria*. A comparison of these degenerating *Calluna* zones with those outside large spreading *Carex* associations on the heaths where the *Calluna* is degenerating and the *Carex* is spreading confirmed the belief that these degenerating *Calluna* zones had similar origins, the degeneration of the *Calluna* and spread of the *Carex* being in both cases due to rabbit-attack on the *Calluna*.

The presence of *Carex arenaria* around some collections of rabbit burrows in the *Calluna* heath, although it was absent elsewhere, and its absence around other collections of rabbit burrows whilst it was present elsewhere, thus appeared to be due to the following series of events. Some rabbits originally made a collection of burrows in the *Calluna* heath and brought about the degeneration of the immediately surrounding *Calluna* (see Part II, Pl. VI, Photo. 1). After the surrounding *Calluna* had degenerated, *Carex arenaria* colonised this area relatively bare of *Calluna*, the rabbits eating the more attractive surrounding *Calluna* at the edge of and outside the *Carex* rather than the less attractive *Carex* which was colonising the degenerated area itself; until eventually, owing to the differential action of the rabbits on the *Calluna* and the *Carex*, a fairly large area occupied by *Carex arenaria* on degenerate *Calluna* heath around rabbit burrows in the *Calluna* heath was produced (see Pl. V, Photo. 9). After the *Carex* had colonised these areas the rabbits continued to go to the edge of the more attractive *Calluna* outside the *Carex* for their food rather than eat the relatively unattractive *Carex* which had colonised the area around their burrows. A degenerating *Calluna* zone outside the edge of a spreading *Carex arenaria* association was thus produced¹ (see Pl. V, Photo. 10) and eventually a fairly large area of *Carex* around the collection of rabbit burrows in the *Calluna* heath resulted (see Pl. V, Photo. 9).

¹ Cf. the production by rabbit-attack of a degenerating *Calluna* zone outside the edge of a spreading unattractive *Pteris* association (see p. 7).

It appeared probable also that, as the degeneration of the *Calluna* through rabbit-attack proceeded, and as the resulting *Carex* association increased in diameter, the rabbits from the central burrows eventually had to go so far to reach the more attractive *Calluna* outside the edge of the spreading *Carex* association that, rather than do this, they tended to eat the relatively unattractive *Carex* because it was much nearer to their burrows, thus eventually producing secondary areas around rabbit burrows bare of *Carex* inside the now larger *Carex* associations.

It appeared that if this theory of the origin of the reversed distributions of the *Carex* relatively to the collections of rabbit burrows is true, smaller areas bare of *Carex* would very likely occur around some of the individual burrows in the collection of rabbit burrows which was, as a whole, associated with *Carex arenaria* in the *Calluna* heath. A search for such smaller incipient bare areas around individual burrows in the smaller *Carex* associations was then made and their actual existence was discovered (see Pl. VI, Photo. 11) although they had not been seen before. The actual existence of these small incipient bare areas around individual burrows affords striking confirmation of the theory of the origin of the reversed and apparently anomalous distribution of *Carex arenaria* in relation to the collections of rabbit burrows.

It may be noted that the close association of the *Carex* (seen in Pl. V, Photo. 9) with the collection of rabbit burrows strongly confirms the theory already given (see page 5) that the recent rapid spread of *Carex arenaria* in Breckland and the resulting large *Carex arenaria* associations are associated with and due to the presence of rabbits in the district and their differential action upon the *Calluna* heath and the *Carex*; and do not depend, for instance, upon localised edaphic conditions.

Ordinarily the presence and competition of the *Calluna* prevents the *Carex* from gaining ground on the *Calluna* heaths, but when the *Calluna* heath has partly degenerated from rabbit-attack, *Carex arenaria* can colonise the degenerated area if its seeds are present, the rabbits eating the *Calluna* on the degenerating edge outside the *Carex* association rather than the relatively unattractive *Carex* in the centre. When the *Calluna* has degenerated to a considerable distance from the burrows, the rabbits, rather than go this distance to the *Calluna*, tend to eat the relatively unattractive *Carex* immediately around their burrows, thus producing secondary areas bare of *Carex* around the burrows although the *Carex* is associated with the burrows as a whole.

Thus the reversed and apparently anomalous distribution of the *Carex* in relation to the rabbit burrows is explained. It is the relative distance of the more attractive *Calluna* with resulting variation in the rabbit-pressure on the *Carex* which is the determining factor in the two classes of cases. Both conditions are really different stages fairly wide apart in the same biotic succession. These phenomena are illustrated in the accompanying diagram (Fig. 1). The apparently anomalous case of the

presence of *Carex* immediately around the collection of burrows and its absence elsewhere (see Pl. V, Photo. 9) is developmentally a more primitive condition than the more obvious and apparently more natural case of its absence around the burrows and its presence elsewhere; but when, as often happens, the more attractive *Calluna* has degenerated to a considerable

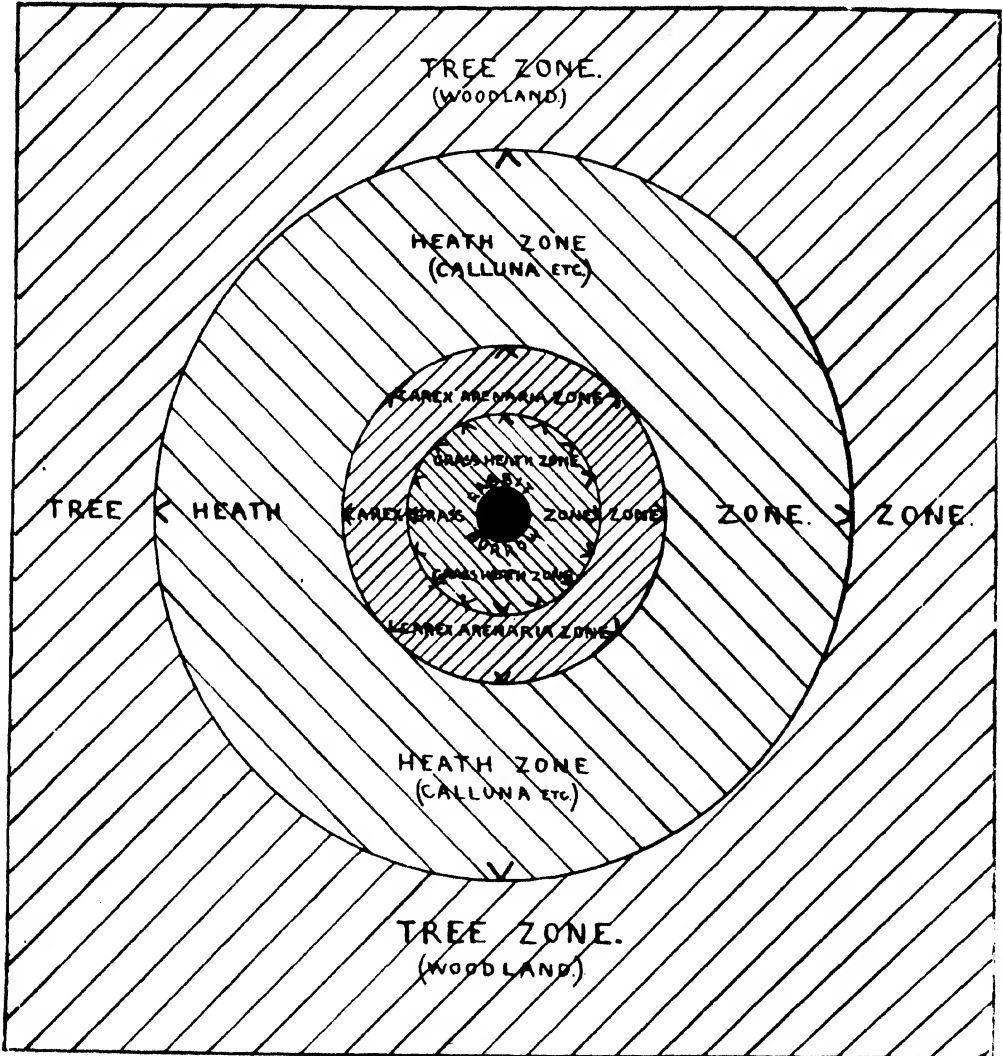


FIG. 1. The Biotic Zonation of Breckland—Zonation of Vegetation around Isolated Rabbit Burrow. For further description see text, pages 10—16.

distance before *Carex* has colonised a particular collection of burrows, the primitive condition of close association of the *Carex* with the collection of burrows may never occur, owing to the rabbit-pressure on the available food being sufficiently great to keep the spreading *Carex* back from the collection of burrows from the first.

When the rabbit-pressure is very great, as on Cavenham Heath, and the *Calluna* heath is degenerating rapidly, the rabbit-pressure is often also sufficient to keep down the *Carex* shoots and practically obliterate the normally intermediate *Carex arenaria* zone which would otherwise become apparent, so that the developmentally intermediate *Carex arenaria* zone is practically absent and the *Calluna* heath appears to degenerate directly to grass-heath. The same effect is observed under conditions of less heavy rabbit-attack when *Carex arenaria* seeds and rhizomes are absent, i.e. in those regions which the spreading *Carex arenaria* has not yet reached.

THE BIOTIC ZONATION OF BRECKLAND.

Examination of the accompanying photographs (Photos. 9, 10 and 11) and the explanation which is given above will make it clear that the effect of the rabbits is to produce a particular zonation in the vegetation immediately around their burrows as is illustrated in the accompanying diagram (Fig. 1, p. 13). The centrifugal order of the various vegetation zones in this zoned vegetation around rabbit burrows in Breckland is as follows: 1. (bare sand and lichens), 2. grass-heath zone, 3. *Carex arenaria* zone, 4. typical heath zone (*Calluna* etc.), 5. tree zone (pine woodland, etc.).

This typical zonation of vegetation around rabbit burrows on otherwise uniform and level sandy tracts in Breckland is a very beautiful and striking example of a dynamic vegetation succession or developmental series of conditions produced by the differential effects of the diminishing intensity of biotic attack upon various types of vegetation as the distance from the rabbit burrows increases.

If the intensity of the radiating rabbit-attack from the burrows gradually increases the various zones in the zoned vegetation around them would gradually expand outwards (as is indicated by the arrow heads in Fig. 1) until eventually practically the whole of the area associated with the burrows would become occupied by dwarf grass-heath vegetation.

If, on the other hand, the radiating intensity of the rabbit-attack from the burrows gradually diminished the various zones in the zoned vegetation around them would gradually contract and close up to the centres until eventually practically the whole of the associated sandy area would become occupied by pine woodland.

It is thus seen that variation in the intensity of the rabbit-attack alone is sufficient to change the dominant type of vegetation in Breckland from pine woodland to dwarf grass-heath vegetation through the phases of *Calluna* heath and *Carex arenaria*, and that for each given intensity of rabbit-attack there is a certain associated vegetation. In other words, if the rabbit-attack were non-existent or very slight, pinewood would be the dominant type of vegetation on a particular area. If the intensity of the rabbit-attack were

slightly greater and remained at a certain constant level *Carex arenaria* would tend to be the dominant type of vegetation on the area, and if the intensity of the rabbit-attack were much greater still, grass-heath would tend to be the dominant type of vegetation on the area.

It should be noted however that the presence of *Pteris aquilina* in any locality interferes with the typical biotic zonation of Breckland, for although *Pteris* cannot dominate grass-heath under conditions of extremely heavy rabbit-attack yet it can dominate *Carex* and *Calluna* under all intensities of rabbit-attack.

The following theory to account for this production of zoned vegetation around rabbit burrows in Breckland may possibly be interesting. Suppose the amount of rabbit-attack emanating from the burrows to be gradually reduced to zero, then the *Carex arenaria* of the *Carex* zone which can grow taller than the grasses would gradually invade and smother the more dwarf grasses of the grass-heath zone, and the central grass-heath zone would eventually disappear. The *Calluna* of the *Calluna* zone which can grow taller than the *Carex* would gradually invade and smother the more dwarf central *Carex* zone and the central *Carex* zone would eventually be obliterated. In the same way the pine trees of the outer pinewood zone would gradually colonise the central *Calluna* zone and would eventually smother the more dwarf *Calluna*¹. Probably the enormous advantages that plants which can grow tall possess in being able to dominate and often eventually to exterminate more dwarf competitors largely no doubt owing to interception of the light are not sufficiently emphasised in the existing literature relating to vegetation. Although tall growing plants possess enormous potential advantages over more dwarf competitors yet it will be noticed that all the different kinds of plants concerned in this zonation accord with the generalisation already given on page 3, that taller growing plants eventually suffer more from increasing biotic attack than do more dwarf growing competitors. Increasing biotic attack has the effect of an increasing downward pressure on associated vegetation. It will be noticed that there is an upward gradation in height of the different types of vegetation as the distance from the rabbit burrow increases. Suppose now the biotic attack from the burrows to rise gradually from zero to a maximum. The pinewood round the burrows would eventually disappear owing to death of the old trees and continual destruction of the individual seedlings. The resulting open and well-lighted space could eventually become colonised by the more dwarf *Calluna* which does not suffer so much from the biotic attack as do the seedling trees. When the rabbit-attack immediately around the burrows became greater the *Calluna* heath itself in this position would degenerate and would be replaced by the more dwarf *Carex arenaria*. As the biotic attack from the burrows gradually

¹ Cf. the occurrence of *Calluna* in well-lighted spots in woods. Tansley, A. G. *Types of British Vegetation*, 1913, p. 99.

increased the above zones would gradually expand outwards, and the central portion of the *Carex arenaria* association immediately around the burrows would eventually degenerate to still more dwarf grass-heath. Thus the characteristic biotic succession and zonation of the vegetation around rabbit burrows in Breckland would be produced. It will be seen that, if the above theory is true, this interesting zonation largely arises owing to the opposition between the more injurious effects of biotic attack upon taller growing plants and the advantages which taller growing plants would normally possess over more dwarf growing competitors, and that the conditions of the zonation at any time largely represent the effects of a balance between these two opposing influences. Probably there are many other zonations and successions in natural vegetation which depend for their existence upon the opposition and balance between the more injurious effects of biotic attack upon taller plants and the otherwise natural advantages of tall growth. *Indeed the zonation and present dominance and distribution of the different types of natural and semi-natural vegetation in the various parts of the uncultivated portions of the British Isles and of other countries which have been subjected to a large amount of biotic attack by grazing animals may largely depend upon variations in the intensity of the biotic attack in different regions producing variations in the balance between the progressively more injurious effects of increasing biotic attack upon the taller kinds of plants and the great natural advantages which the taller growing plants otherwise possess over their more dwarf competitors.*

SUMMARY AND GENERAL REMARKS.

It is thus seen that in addition to causing the main *Calluna* heaths to degenerate to grass-heaths, which rapidly revert to Callunetum on protection from rabbits, these animals also produce various other striking effects upon the vegetation. One of their most important effects is that they are especially injurious to taller growing plants and to inflorescences. *Campanula rotundifolia* and many other plants are entirely prevented from flowering.

The rabbit-attack tends to reduce greatly the number of species of plants present on any area and is especially destructive to various dicotyledonous species, thus tending to favour the growth of grasses relatively to dicotyledons.

The rabbit-attack also limits tree growth to the damper valleys where the young trees can grow comparatively vigorously while if it were not for the rabbit-attack tree growth could spread over and dominate the upper areas.

In addition to attacking the *Calluna* heaths, grass-heaths, and young trees the rabbits also attack the large *Carex arenaria* and *Pteris aquilina* associations which are common in Breckland, and the possible and actual distributions of all these plant associations are very greatly modified by the differential effect of the various intensities of rabbit-attack upon the various competing species. Indeed the chief characteristic of the vegetation of Cavenham Heath is the extreme mobility of the various plant associations

due to the differential action of varying intensities of rabbit-attack upon them in upsetting the balance and thus altering the ultimately dominant types of vegetation.

The vegetation of Blakeney Point is also considerably more mobile than might have been suspected¹. Probably the changes in the vegetation due to topographical changes are more rapid at Blakeney Point than on Cavenham Heath owing to the presence of mobile shingle banks and sand dunes in the former case; but on the other hand, the general changes in the vegetation are far more rapid on Cavenham Heath than on Blakeney Point owing to the greater operation of biotic factors on Cavenham Heath which completely outweighs the comparative absence of topographical changes.

The different intensities of the biotic attack at varying distances from the rabbit burrows produce a characteristic zonation of the vegetation around the burrows on the otherwise uniform sandy plains of Breckland. This zonation is a very striking and beautiful example of a dynamic biotic succession depending for its existence upon the different amount of biotic attack at various points. The existing dominances of the different kinds of vegetation on their various zones around the burrows, and also the existing dominances of the corresponding kinds of vegetation on the ground occupied by the corresponding large *Calluna* heaths, *Carex arenaria* and grass-heath associations of Breckland, ultimately depend for their existence and maintenance upon the existence and maintenance of different intensities of biotic attack upon the vegetation of the corresponding areas, and the respective dominances of these different kinds of vegetation do not depend upon specially localised differences in the soils.

The very complex distributions of these various plant associations on different areas in Breckland was for long unexplained, but we now know that they primarily represent individual developmental phases in a particular degenerative succession of taller vegetation due to the varying intensity of biotic attack at different points².

Ecological factors are sometimes grouped solely as climatic and edaphic, but the highly important biotic factors which are capable of exerting such great influences upon vegetation should probably always be included in the classification, and the extent to which they are or have been present in

¹ Oliver, F. W. "Blakeney Point in 1913." This JOURNAL, 1, 1913, p. 4.

² It is instructive to realise that much time might have been wasted in the first place in examining and analysing the soils under the different plant associations in Breckland on the supposition that the differences in the vegetation were due to differences in the soils. Various differences in the water contents, etc., of the different soils would undoubtedly have been detected, but these particular differences would have been largely consequent upon the occupation of the soils by different kinds of vegetation (owing to differing intensities of biotic attack) and not *vice versa*. These considerations emphasise the advisability when beginning an ecological study of a particular area of spending at first a considerable time in looking round and collecting general information before embarking on laborious work on the basis of merely preliminary hypotheses.

particular cases and their effects should probably always be considered when dealing with the existing zonation and distribution of natural and semi-natural vegetation in any district. Apparently the presence of rabbits alone is sufficient to change the dominant vegetation of Breckland where *Pteris* is absent from pinewood through *Calluna* heath and *Carex arenaria* associations to dwarf grass-heath.

Note on the Effects of Rabbits upon the Vegetation of West Newton Heath, near Sandringham, in North-west Norfolk.

Although rabbits often produce areas bare of *Carex* around collections of their burrows in the dense *Carex arenaria* associations of Breckland, the writer has not yet seen areas bare of the highly unattractive *Pteris* around individual collections of rabbit burrows in the *Pteris* associations of Breckland. Apparently the rabbits eventually prefer to migrate right outside of the spreading *Pteris* associations to a region with more attractive food, rather than to eat the unattractive *Pteris* when it has spread a long way all around their burrows. In Breckland, they are apparently always eventually able to find a more suitable region with more attractive food to migrate to and so are able to avoid ultimately having to eat the unattractive *Pteris*.

The writer has however seen areas bare of *Pteris* around rabbit burrows in a *Pteris* association on West Newton Heath near Sandringham in North-west Norfolk (see Pl. VI, Photo. 12). The rabbits are much less numerous per unit area on this heath than they are on most of the Breckland heaths, but in spite of this, if they are so hungry that they have to eat the very unattractive *Pteris* around their burrows in this locality, the actual rabbit pressure on the vegetation of West Newton Heath must be far greater than that on the Breckland heaths where the phenomenon does not occur. If, in spite of the relatively few rabbits, the actual rabbit-pressure on the vegetation of this North-west Norfolk heath is far greater than that on the Breckland heaths, the results of rabbit-attack observed in Breckland may have a wider application than might otherwise have appeared to be the case. Probably the heavier rabbit-pressure at the present day on the vegetation of West Newton Heath largely arises out of the fact that most of the vegetation now consists of unattractive *Pteris aquilina* and of unattractive *Erica tetralix* so that the rabbits have to eat these plants, and any more attractive plants which remained would probably be very quickly suppressed. The extensive distribution and the great purity of the unattractive *Erica* and *Pteris* associations on West Newton Heath at the present day are thus probably largely due to the cumulative effect of rabbit-pressure in bringing about the degeneration of any more attractive previous plant associations and in ultimately severely eating off more and more rapidly as they became rare any isolated relatively attractive plants amongst the mass of unattractive vegetation.



Photo 1. RABBIT-PROOF FENCE ACROSS THE SOUTH SIDE OF CAVENHAM HEATH, WESTERN END. Note difference in the vegetation on the two sides. On the protected side there are many inflorescences, while on the unprotected side there are no inflorescences, the vegetation is nibbled closely down and much bare sand is exposed. (See page 2 of the text.)

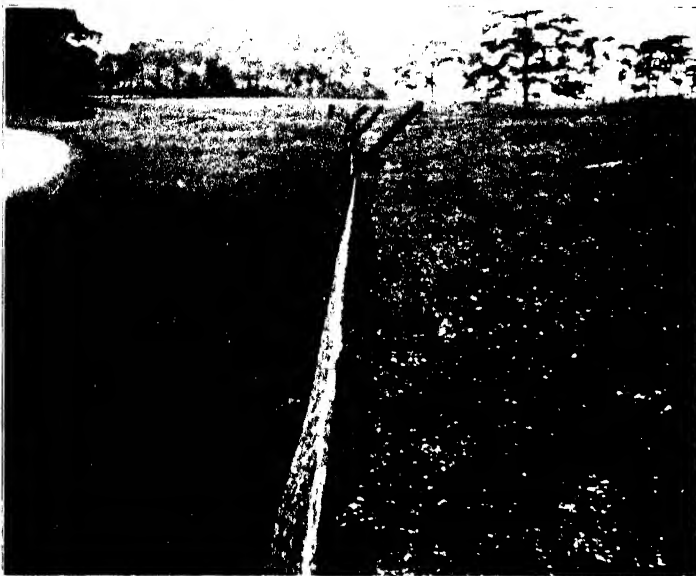


Photo 2. SOUTHERN RABBIT-PROOF FENCE ON CAVENHAM HEATH, EASTERN END (looking in the opposite direction to Photo. 1). Note greater difference in the luxuriance of the vegetation on the two sides. Explanation of this greater difference is given in the text. Note presence of *Carex arenaria* on the protected side of the fence and its absence on the rabbit attacked side. (See page 2.)

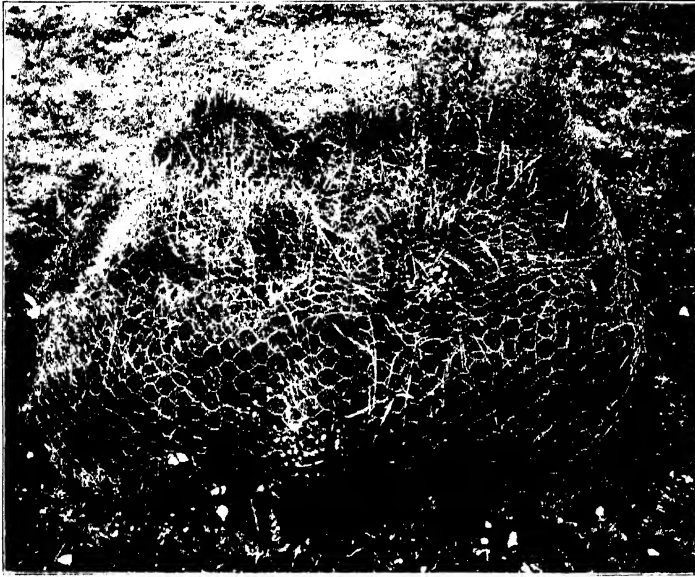


Photo 3. *SEDUM ALBUM* FLOWERING INSIDE THE RABBIT-PROOF CAGE ON THE RELATIVELY PROTECTED SIDE OF THE FENCE. The *Sedum album* flowers can be well seen in the photo, while outside the cage no flowers of this plant occur although the plant itself is freely present. There are also far more *Crepis*, *Carex*, *Agrostis*, *Festuca* and *Holcus* inflorescences inside than outside the cage and the vegetation is considerably more luxuriant as can be seen in the photo. (See page 3.)



Photo 4. *GALIUM VERUM* FLOWERING INSIDE RABBIT-PROOF CAGE. *Galium verum* flowers inside the cage can be well seen in the photo, while outside the cage flowers of this plant are very scarce and those which do exist are very poor. (See page 3.) Note also the luxuriance of the vegetative portions of the *Galium* inside the cage. Outside the cage the vegetative portions of this plant are eaten down very closely by the rabbits.

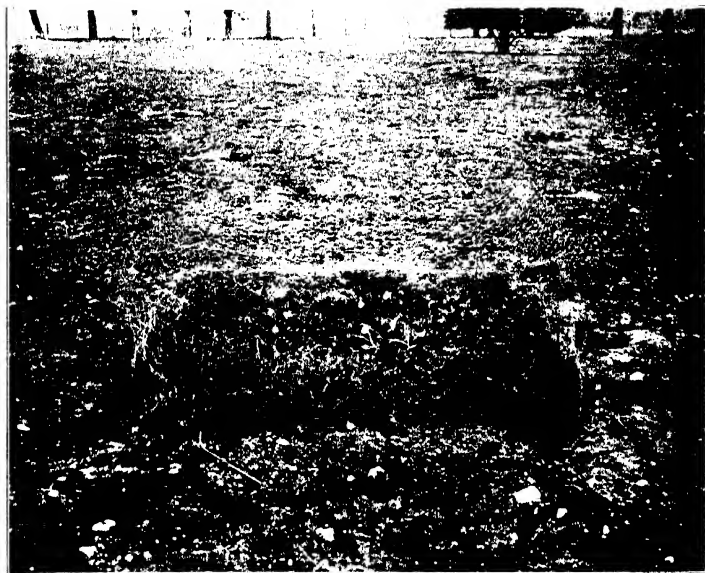


Photo 5. RABBIT-PROOF CAGE ON MIDDLE OF THE DEGENERATE GRASS-HEATH ASSOCIATION. Note *Campanula rotundifolia* flowers inside the cage 'show whitish' although there are none outside for a very great distance all around. (See page 4.) Note the very vigorous and flowering young *Calluna* stems inside the cage. The grass heath association inside the cage, which was formerly *Calluna* heath, is very quickly going back to *Calluna* heath now that the rabbit-pressure is removed. (See page 4 of the text.)

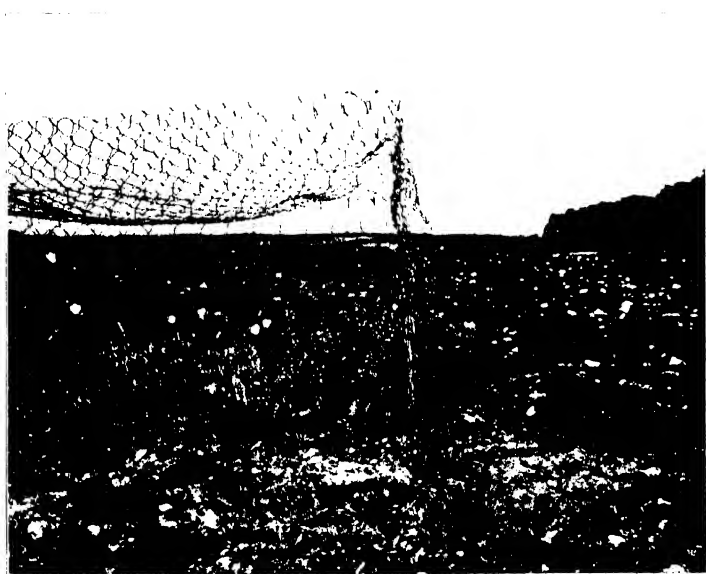


Photo 6. *CAMPANULA ROTUNDIFOLIA* FLOWERS AND VIGOROUS FLOWERING YOUNG *CALLUNA* STEMS 20 CMS. HIGH INSIDE RABBIT-PROOF CAGE. The large white objects inside the cage are *Campanula* flowers and the small whitish specks are *Calluna* flowers. The large white objects outside the cage are bared flints, many of them being prehistoric flint implements. Outside the cage any *Campanula* inflorescences and *Calluna* stems are nibbled down very closely to the surface of the sandy soil and are quite unable to produce flowers as can be well seen in the photo. (See page 4.) Note the closely nibbled down and almost flat *Calluna* hummock on the right of the photo, in line with the front of the cage.

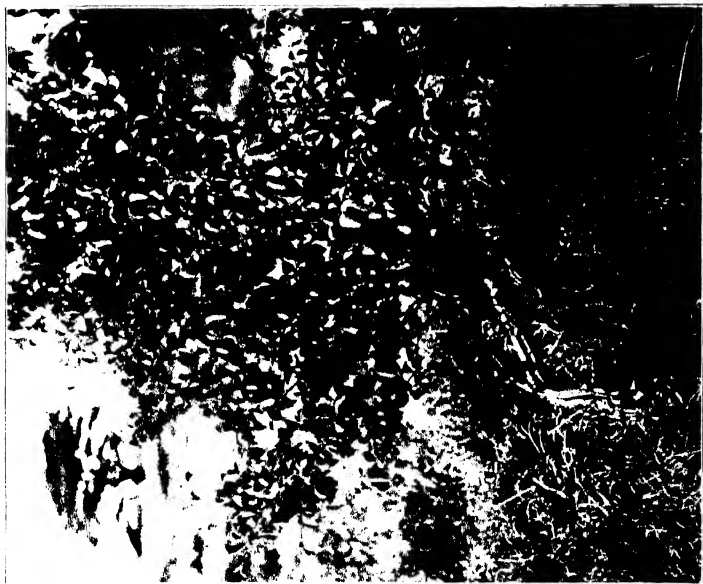


Photo 8. YOUNG *BETULA ALBA* TREE ON VALLEY SIDE WITH STEM BADLY ATTACKED BY RABBITS. Note that the stem has become badly contorted as a result of the rabbit-attack probably owing to uneven release of internal stresses consequent upon uneven eating by the rabbits.

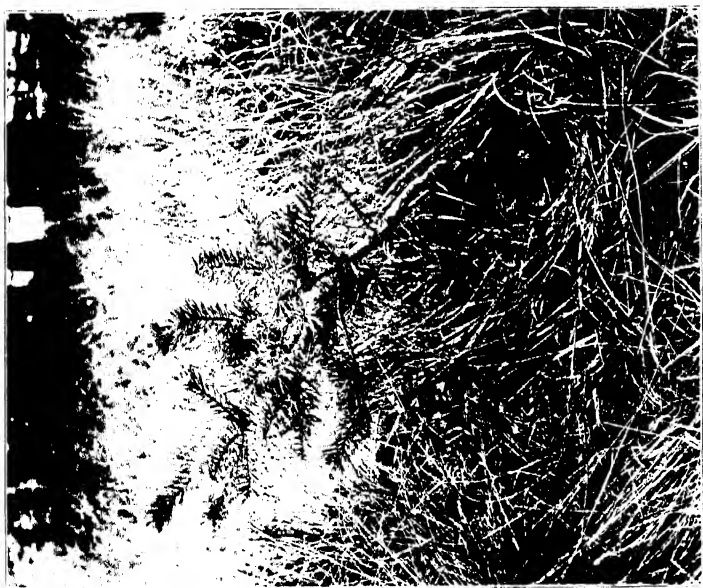


Photo 7. YOUNG *PINUS SYLVESTRI*S TREE IN VALLEY WITH STEM BADLY ATTACKED BY RABBITS. The rabbit-attacked stem can be well seen. It is doubtful if this particular tree will be able to survive the rabbit-attack but it may possibly do so. (See page 9.)

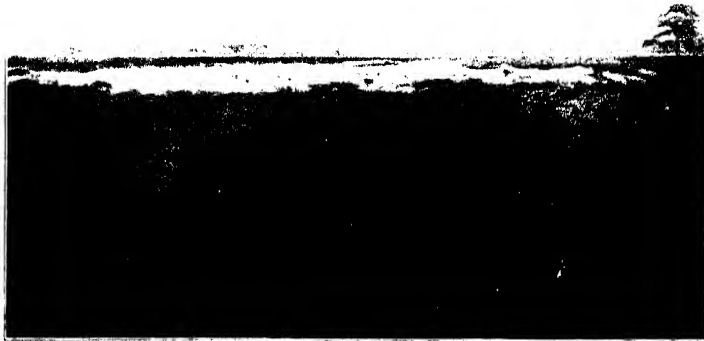


Photo 9. AREA OCCUPIED BY A RELATIVELY SMALL DENSE *CAREX ARENARIA* ASSOCIATION AROUND A COLLECTION OF RABBIT BURROWS IN A *CALLUNA* HEATH—TUDDENHAM HEATH. The photo. shows a phenomenon which is of very great interest in view of the fact that the presence of the *Carex arenaria* around the collection of rabbit burrows and its absence elsewhere appears to be exactly the opposite to the frequent and apparently more natural instances in which the *Carex* is absent around the collections of rabbit burrows while it is present elsewhere. (See page 10.)



Photo 10. TRANSITION ZONE ON EDGE OF A *CAREX ARENARIA* ASSOCIATION AROUND A COLLECTION OF RABBIT BURROWS IN A *CALLUNA* HEATH. (Note also *Carex arenaria* around another collection of rabbit burrows in the middle distance.) Note that the *Carex arenaria* shoots and leaves gradually become fewer in number, less in height and weaker in this transition zone, occurring chiefly along the rabbit tracks, while the *Calluna* bushes gradually become greater in height as the typical *Calluna* heath is entered. This is a rather narrow zone of *Calluna* heath degenerating through rabbit-attack but a generating zone of *Carex arenaria* is associated with it. (See page 10.)

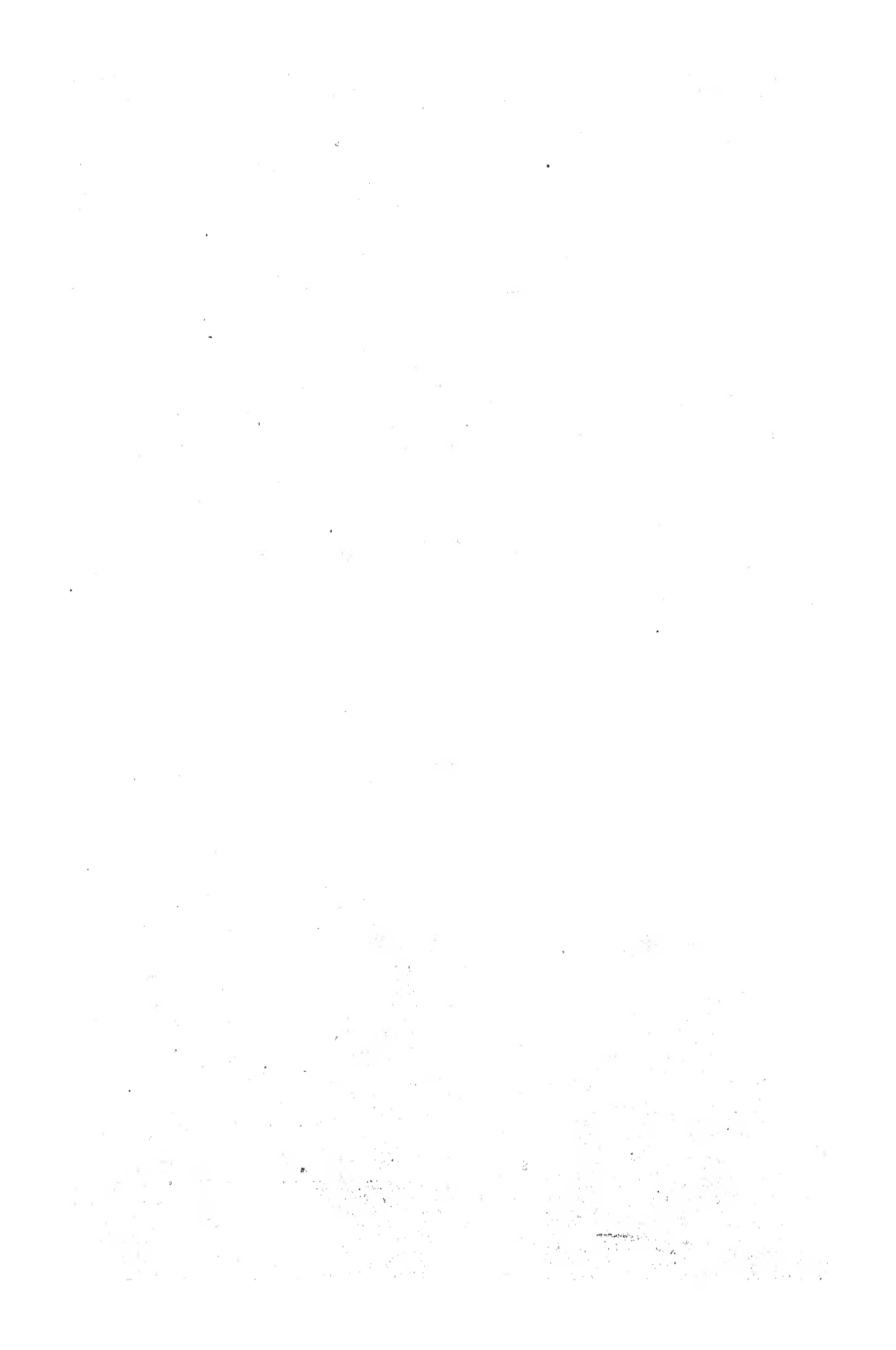




Photo 11. SMALL INCIPIENT GRASS-HEATH AREA BARE OF *CAREX* AROUND INDIVIDUAL RABBIT BURROWS IN AN AREA OF *CAREX* WHICH IS, AS A WHOLE, ASSOCIATED WITH RABBIT BURROWS IN *CALLUNA* HEATH. The discovery of these small incipient bare areas around individual burrows affords striking confirmation of the theory relating to the apparently anomalous and reversed distribution of the *Carex* in relation to the collections of rabbit burrows. (See page 12.) Compare the zonation of the vegetation seen in the picture with that indicated in the diagram, Fig. 1, page 13 in the text.

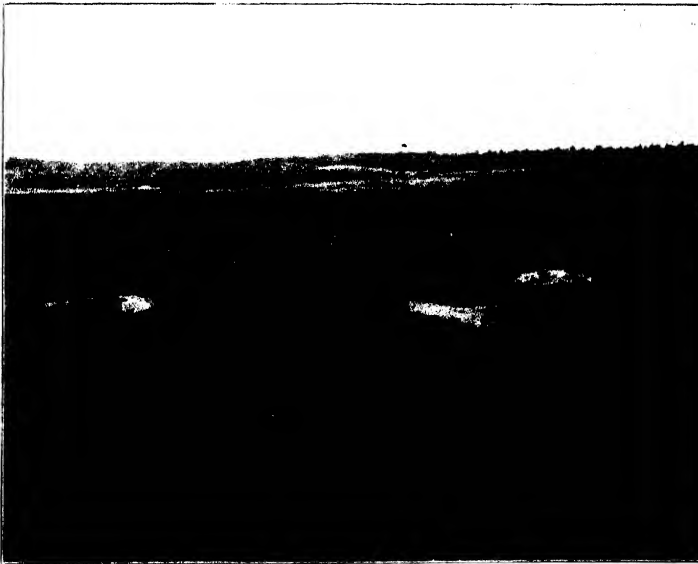


Photo 12. AREA BARE OF *PTERIS* AROUND RABBIT BURROWS IN A *PTERIS* ASSOCIATION ON WEST NEWTON HEATH, NEAR SANDRINGHAM. An area associated with rabbit burrows and almost devoid of *Pteris* fronds can be well seen in the photo. This phenomenon is rare in East Anglia and the writer has not yet seen it in Breckland. (See page 18 of the text.)

PLANT SUCCESSION ON ABANDONED ROADS IN EASTERN COLORADO.

BY H. L. SHANTZ¹.

(With twenty-three Figures in the Text.)

INTRODUCTION.

The natural vegetation at Akron, Colorado, consists largely of two grasses--the Grama grass, *Bouteloua gracilis* (*B. oligostachya*) and the Buffalo grass, *Buchloë* (*Bulbilis*) *dactyloides*. This vegetation, discussed² by the writer as the Grama-Buffalo grass association of the short-grass formation, is the principal type of the central portion of the Great Plains. If turned under by the plough and abandoned after having been cultivated for some time, the native sod will be re-established in from twenty to fifty years. The following stages may be recognized in the succession:

(1) an early weed stage consisting usually of comparatively large plants, scattered and far enough apart not to compete with each other for soil moisture;

(2) a late weed stage, a dense growth of stunted plants, the amount of growth indicating the total amount of water which was available for growth;

(3) a short-lived grass stage;

(4) a perennial stage;

(5) an early short-grass stage; and

(6) a late short-grass stage leading to the fully re-established typical short-grass sod.

The succession on abandoned roads differs from that on abandoned fields only in minor details.

FORMATION OF ROADS.

Roads were formed by vehicles driven over the short-grass sod in the same trail until the grass and sod were worn off and the soil exposed (Fig. 1). Continued use of the same trail lowered the level, partly by packing, but more largely by the gradual removal by wind of the dust particles loosened

¹ Published with the permission of the Secretary, U.S. Department of Agriculture.

² H. L. Shantz, "The Natural Vegetation as an Indicator of the Capabilities of Land for Crop Production." U.S. Department of Agriculture, Bureau of Plant Industry, Bull. No. 201, 1911.

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by the wheels of vehicles or the feet of the horses. In this way a road was considerably lowered in the course of three or four years. At this stage the road consisted of two worn trails and the central portion, which was still sodded, since few one-horse vehicles were used (Fig. 1).

When this country was first settled roads or trails led directly from one point to another, there having been no fences to interfere with travel. As fences were erected these angling roads were necessarily abandoned and new roads formed which followed the section lines.



FIG. 1. Road on the High Plains in Eastern Colorado. This road is used by both single and double vehicles. The wheel tracks at the extreme right of the picture are of a double vehicle. Those next to the left are of a single vehicle, the horse travelling just to the left of the central strip of untouched grass. At the left a new road is being formed before the old one is abandoned. The vegetation in the old road has been entirely worn off except in the right centre where the native short-grass is almost undisturbed. At the left in the new road the vegetation is completely destroyed in the wheel tracks but a broad strip remains in the middle. The effect of this road on the adjacent vegetation is shown by the more luxuriant growth and the fact that the vegetation remains green longer than that of the untouched sod. Photographed Sept. 17, 1913.

Even where fences were not constructed the old roads were often abandoned. During rainy periods these roads became muddy and were less desirable for travel than the adjacent sod. In turning aside to secure a better track and thus escape the mud in the old track, one horse was pulled to the edge of the road and the other on to the sod of the middle of the road. In this way two new trails were soon formed, one in the centre and the other at the edge of the old road (Fig. 8). Roads where travel was comparatively

heavy were usually worn down more uniformly. In such cases the new road was formed at the side of the old (Fig. 2).

When once abandoned the trails were seldom used again, and new roads were seldom found on but one side of the old road. The explanation of this fact seems to be as follows: When two teams on the second road meet it is much easier for the team to turn out on the sod at the side of the road than into the old road because of the two "ruts" forming the latter. To

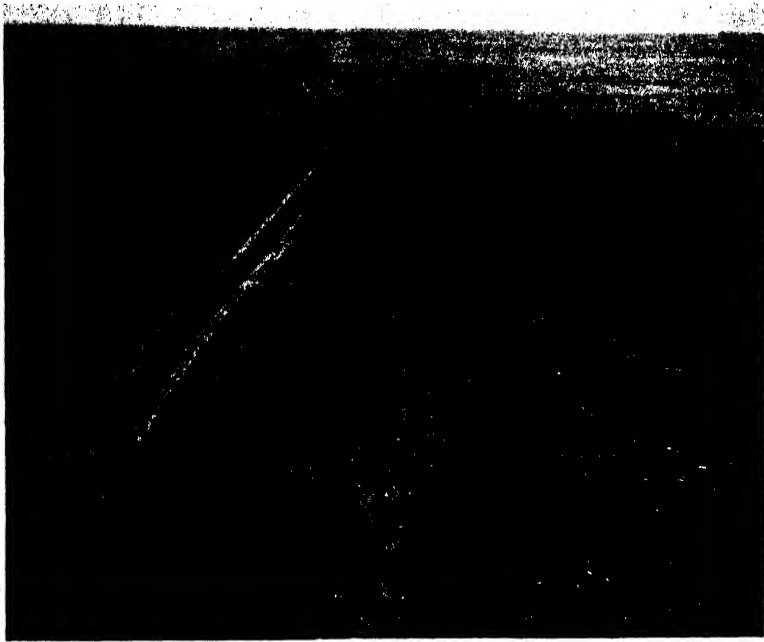


FIG. 2. Road on the right abandoned, road on the left still in use. The old road has been lowered from three to twelve inches and the greater portion of the vegetation destroyed. It has been abandoned one season. The original native vegetation at the edge of the road shows increased growth due to increase in available soil moisture. The vegetation in the old road consists of a few plants of *Gutierrezia sarothrae* and *Artemisia frigida* which have maintained life throughout the period when the road was in use. These are now becoming prominent features in the vegetation. The new plants which have appeared during the one year in which the road has been undisturbed are of the weed stage and are *Salsola pestifer*, *Malvastrum coccineum*, *Amaranthus graecizans*, *Polygonum aviculare*, and *Schedonardus paniculatus*. Vegetation is very sparse. Plants of later stages are present only as remnants of the undestroyed old vegetation. Photographed Sept. 17, 1913.

use the old side would necessitate driving over these two deep tracks and would occasion considerable extra jar and no little inconvenience. As a result the team driving with the old road on the right would keep its place, or at most only turn partly into the old road, while the one with the old road on the left would turn out on to the new sod. (It is customary in the United States to turn to the right.) By continuing to drive on the sod a new road was soon formed at the side of the old. When for any reason

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a team was turned aside it was always to the adjacent native sod rather than across the old ruts.

In this way a new road was formed which ran parallel to the old roads. In some places a large number were formed (Figs. 3--6). Occasionally the number of roads varies, due to the continued use of part of the old road, while at other points a new road had been formed. This condition is rarely found, except where the roads cross waterways. In such places the number

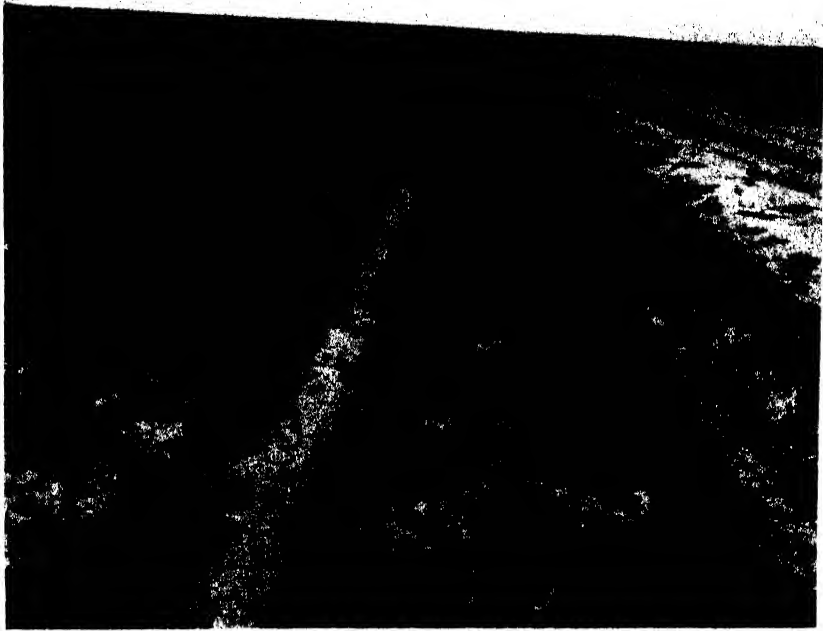


FIG. 3. A general view of a series of ten parallel roads which have been used successively since 1893. The newest road (No. 0) is at the right and was first used in 1914. The next road (No. 1) to the right of the centre of the picture was first used in 1913 and abandoned in the spring of 1915. The roadway in the centre of the picture (No. 2) was abandoned in 1914, and the vegetation which represents two seasons' growth is principally *Polygonum aviculare*. The next road (No. 3) is dominated largely by *Polygonum* but has also numerous plants of *Schedonnardus* and occasional plants of *Gutierrezia*. Road No. 5 shows a marked change in vegetation and is dominated by *Schedonnardus* with *Gutierrezia* quite abundant. The sixth road is dominated by *Schedonnardus* and *Gutierrezia*, with *Buchloë* rapidly pushing in from the sides. Photographed June 30, 1915.

of roads is usually reduced. Often the change from the old to the new road was gradual, both being used simultaneously for a time (Fig. 1) and the old road finally abandoned (Fig. 2). It often happened that after the second road had been formed new roads were formed by driving with the inner wheel in the outer of the tracks, and with the outer wheel on the sod (Fig. 9). This would come about naturally by the team not completely returning to the old road after having given half in passing another vehicle. Where so few vehicles pass that one seldom, if ever, had

to turn aside, as on some of the less frequented roads, this type of road was often developed, by turning half aside to avoid the mud of the well-beaten trails. In this way trail after trail was added until many were formed, ranging in age from the oldest on one side to the newest on the other side (see Fig. 10).

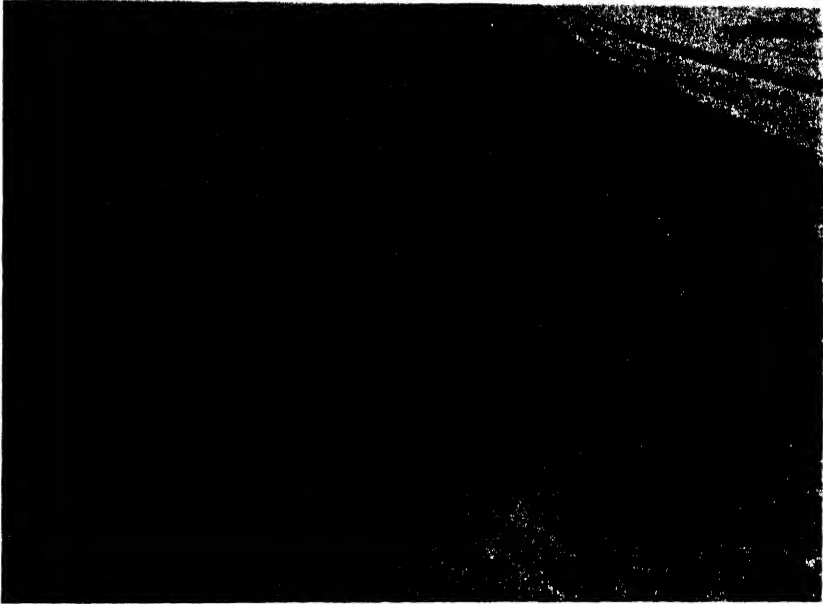


FIG. 4. A general view of the same series of parallel roads shown in Fig. 3, but photographed two years earlier. The oldest road (No. 9) is at the extreme left and the newest (No. 1) at the extreme right. Two of these roadways (Nos. 2 and 1) are now in use, the oldest of which is clearly shown in the figure. These new roads show no vegetation except an occasional plant of *Polygonum aviculare*. The third youngest road in the right foreground shows a rather dense population of *Polygonum aviculare* with occasional plants of *Salsola pestifer* and *Gutierrezia sarothrae*. The fourth road differs from the third only in the occasional occurrence of *Grindelia squarrosa* and *Schedonnardus paniculatus* and a greater number of young *Gutierrezia sarothrae* plants. The fifth road shows a marked change in vegetation. The weed stage is represented by an occasional *Grindelia squarrosa* plant and the vegetation is dominated by *Schedonnardus paniculatus* and *Gutierrezia sarothrae*. The sixth road is dominated by *Gutierrezia sarothrae* and *Schedonnardus paniculatus*. *Buchloë dactyloides* has pushed runners in at the edge for more than a foot. Grazing animals have aided in reducing the amount of growth of the weeds on roads 3 and 4. Photographed Sept. 20, 1913.

Loose cattle or horses have often formed trails approximately parallel to the roads. In such cases the oldest are usually at one side, and as the other side is approached they become successively newer (Fig. 18). These trails can easily be distinguished from the true roads by the fact that the trails are not strictly parallel (see right and left of Fig. 17 and left of Fig. 15).

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These are probably formed by several cattle travelling abreast. Those following the wheel tracks continue in a straight course while those forming the new trails parallel the wheel tracks only approximately.

The age of the vegetation on many of the roads can be told with considerable accuracy, since it is possible to ascertain when certain fences were constructed and traffic stopped.



FIG. 5. Roads 7, 8 and 9 of the series shown in Figs. 3 and 4. Road 7 at the left is dominated by *Gutierrezia sarothrae* but *Schedonnardus paniculatus* is still an important plant. Unimportant plants are *Grindelia squarrosa*, *Festuca octoflora*, *Malvastrum coccineum* and *Sporobolus cryptandrus*. An occasional plant of *Buchloë dactyloides* has become established and runners have pushed in from the side of the road. Many of the *Gutierrezia sarothrae* plants are dying. Road 8 in the right foreground is dominated at the right and left sides by *Buchloë dactyloides*. With this occurs *Grindelia squarrosa* and occasional living and many dead plants of *Gutierrezia sarothrae*. The middle portion of the road is dominated by *Gutierrezia sarothrae*, many plants of which are dying, and by many plants of *Schedonnardus paniculatus* and an occasional plant of *Buchloë dactyloides* and *Sitanion hystrix*. Road 9 shown at the extreme right, and which was first used in 1893, is almost completely resodded with *Buchloë dactyloides*, except in the very central portion which shows a vegetation of *Buchloë*, *Gutierrezia*, and an occasional *Schedonnardus*. *Gutierrezia* plants nearest the *Buchloë* are usually dying. Apparently these roads have been formed at the rate of about one in three years. The younger roads were probably formed more rapidly because of increased use during later years. In that case the age of the vegetation on these roadways is about as follows: Road 1, not abandoned; road 2, not abandoned; road 3, abandoned in 1912 (one year); road 4, in 1911 (two years); road 5, in 1908 (five years); road 6, in 1905 (eight years); road 7, in 1902 (eleven years); road 8, in 1899 (fourteen years); road 9, in 1896 (seventeen years). Photographed Sept. 20, 1913.

REVEGETATION.

The two roads shown in Fig. 1 are still in use. The vegetation has been destroyed only in the two paths, the central portion still retaining its original short-grass cover. Another strip of undisturbed short-grass lies between the new and the old road, the former showing the sod only partially destroyed in the wheel tracks. The only change in vegetation due to the road is found in the better growth of the short-grass at the edge of the road during dry years. Often it fruits along the road when it has not even flowered in the



FIG. 6. Road 9 in the foreground and younger roads at left. Vegetation of road 9 shows almost pure *Buchloë* cover with remnant of *Gutierrezia* stage showing in places in the centre. Younger roads at the left show *Gutierrezia* stage. Note the narrow ridge of natural sod between the roads. Natural *Buchloë-Bouteloua* sod at the right. Photographed Sept. 20, 1913.

natural sod. A narrow green strip of grass is usually evident at the edge of the road after the natural sod is entirely dry. This is due to the reduced vegetative cover, and while the area for the absorption of rain is as great as ever the demand on soil moisture is reduced to the strip of short-grass in the centre and along the edges. Loss of water by direct evaporation from the soil is slight¹ as compared with that lost by transpiration from the

¹ This is true whether the surface of the road be covered with a dust mulch or be bare hard surface.

See **W. W. Burr** (1914), "Storage and Use of Soil Moisture." Research Bulletin No. 5 of the Agricultural Experiment Station of Nebraska, p. 61. Also, **Romistov, V. G.** (1913), "The Nature of Drought According to the Evidence of the Odessa Experiment Field." M.L. and A. Department of Agriculture, Odessa, 1913, p. 17.

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plants and therefore conditions for soil moisture conservation are more favourable in the roads than in the undisturbed sod.

A somewhat later stage is shown in Fig. 2. The old road has been worn almost completely bare and abandoned since the previous summer. A few perennials, chiefly *Gutierrezia sarothrae* and an occasional *Artemisia frigida*, which were not entirely killed by the trampling are now making a good

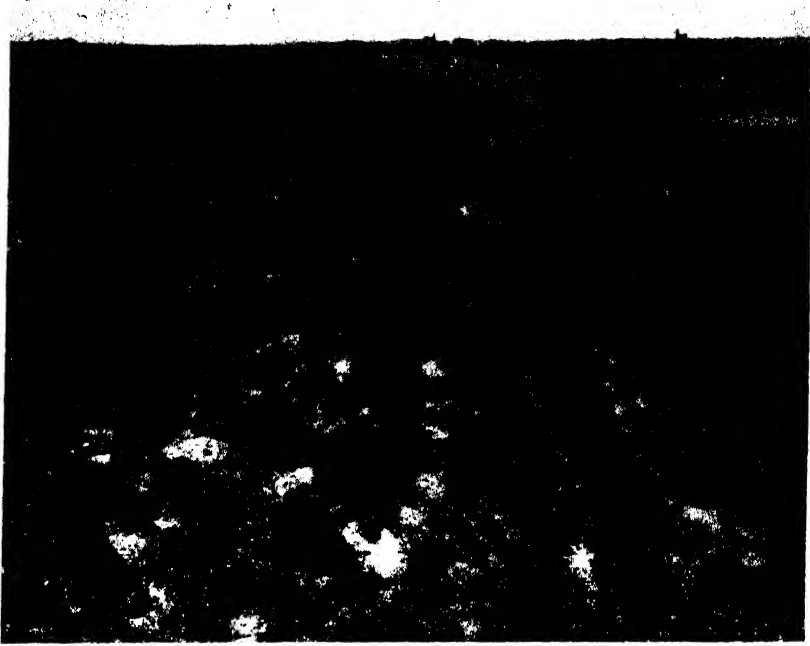


FIG. 7. Three roads used before road 9 of Figs. 5 and 6 was formed. A fence constructed across the roads shown here caused the formation of road 9 in 1893. The road at the right was formed in 1886; seven years later in 1893 all were abandoned. Road 10 at the left of the figure was only slightly used. Roads 11 and 12 were almost equally travelled when abandoned. Road 12 was apparently abandoned some years before roads 10 and 11 and shows a somewhat older vegetation. It seems safe to assume that road 12 was abandoned about three years before 10 and 11. Hence 10 and 11 were abandoned in 1893, or twenty years, and road 12 about 1889, or twenty-three years. Road 10, which is the youngest of these three (20 years), is almost completely resodded by *Bouteloua gracilis* and *Buchloë dactyloides*, due to the incomplete destruction of these plants before the road was abandoned. Road 11 (20 years) shows almost pure sod of *Buchloë* and *Bouteloua* but also many living and dead plants of *Gutierrezia sarothrae*. Road 12 (23 years) shows practically a pure *Buchloë-Bouteloua* sod with a few living and dead *Gutierrezia* plants. Photographed Sept. 20, 1913.

growth. The following plants have already begun to colonize the old road: *Salsola pestifer*, *Amaranthus graecizans*, *Polygonum aviculare*, *Malvastrum coccineum*, *Schedonnardus paniculatus*. With the exception of the last two species these plants represent the weed or first stage in revegetation. At the time the photograph was taken no available soil moisture was found in the native vegetation at the side of this road. In the new trail less than

two per cent. of water was available in each of the surface three feet. During the early season the vegetation which had at that time not been destroyed removed much of the soil moisture. The abandoned road showed from six to nine per cent. of water available in each of the surface three one-foot layers.

In Fig. 8 is shown a road abandoned but one season. The revegetation is very slight, with only an occasional plant of the ruderal stage, such as *Grindelia squarrosa*, *Polygonum aviculare* and *Schedonnardus paniculatus*.



FIG. 8. Road abandoned one season. The central track used principally by a single horse shows incomplete destruction of short-grass sod. The two main travelled tracks are practically bare except for an occasional plant of *Polygonum aviculare*, *Schedonnardus paniculatus*, and *Grindelia squarrosa*. The trail at the left is the result of driving a single rig with the horse in the left main track. If this road had been used for a period of years the new trails would undoubtedly have been formed at the left. Photographed Sept. 20, 1913.

The old road in Fig. 9 has been abandoned for three years. The stage of revegetation is what may be called a late weed stage. While weeds do not play as important a part on abandoned roads as on abandoned tilled land, still the first plants to enter these roads are often the same as those of abandoned fields. Roads are more likely to be occupied by plants naturally occurring in the short-grass but which only now and then spring into prominence. In this figure *Grindelia squarrosa* is a prominent plant, although this prominence is only temporary. Had the photograph been taken one year before or one year later this plant would not have been as

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prominent in the succession. About the only other plants are *Polygonum aviculare*, a representative of the weed stage, *Schedonnardus paniculatus*, a representative of the short-lived grass stage, and an occasional plant of *Gutierrezia sarothrae*. At the edges *Buchloë dactyloides* is slowly sending out runners.

In Fig. 11 an old road is shown which has been abandoned nine years. At this point conditions are unusually favourable for revegetation. The central part of the road is in the *Schedonnardus* stage. *Monroa squarrosa* is also associated with *Schedonnardus*. In the background *Gutierrezia sarothrae*



FIG. 9. The old road (three tracks) at the right was abandoned in the spring of 1911. The new road at the left has been used three seasons by teams and automobiles. The vegetation in the old road consists of *Polygonum aviculare*, *Schedonnardus paniculatus*, *Gutierrezia sarothrae* and *Grindelia squarrosa*. Runners of *Buchloë* have almost crossed the narrow tracks in places. Early weed stage. Photographed Sept. 20, 1913.

and *Aristida longiseta* are present in the centre of the road. The sides are dominated by *Buchloë* which forms a rather dense sod area $1\frac{1}{2}$ feet wide on either side. Here in the foreground the vegetation is passing directly to the *Buchloë* stage, *Gutierrezia* having entirely disappeared from the succession.

A road formed in 1890 was abandoned in 1900 due to the construction of a fence directly across its path. Three different sections of this road are presented in Figs. 12, 13 and 14, to emphasize the fact that the rate of development of the succession is not uniform. In the native undisturbed sod, areas

of vegetation occur which belong to an earlier stage in the natural succession. Succession on old roads is much more rapid in some places than in others. Usually where the road passes through a less thoroughly sodded area the revegetation is slow, but where the native sod is a pure even short-grass cover the succession is more rapid.

In Fig. 12 the vegetation is 13 years old and in the *Gutierrezia* stage. There are also a few remnants of the *Schedonnardus* stage.

In Fig. 13 the vegetation, although of the same age, is in the late



FIG. 10. A series of thirteen parallel tracks (about eight roads) east of Otis, Colorado. The newest roads are now used largely by automobiles. The first five tracks are nearly bare. The vegetation of track 6 is largely young *Schedonnardus* and the annuals, *Plantago purshii* and *Leptilon canadense*; of tracks 7 to 9, mostly *Schedonnardus*; and 10 to 13, mostly *Buchloë*. The ridges between the trails are covered with a typical short-grass. The tracks are filled with the fruiting stalks of *Schedonnardus* which have been blown in from the adjacent short-grass sod. This will explain rapid seeding of new trails to *Schedonnardus*. Photographed Aug. 10, 1915.

Gutierrezia stage or early *Buchloë* stage. In Fig. 14 the succession has in the same period of time reached the *Buchloë* stage, although the *Gutierrezia* stage is still found in the right track.

Vegetation sixteen years old is shown on the trails and roads illustrated in Fig. 15, with the exception of the trail at the extreme right which is still used occasionally by cattle. The vegetation of the trails and roads is in the *Buchloë* stage.

A still older road on which the vegetation has returned to the *Bouteloua-Buchloë* stage in 21 years is shown in Fig. 16. This road was used only

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one year and then abandoned. The complete revegetation was doubtless favoured by the incomplete destruction of the original sod.

In Fig. 18 is shown a series of 23 trails formed by cattle and vehicles, the oldest of which is shown at the left front of the photograph. Successively newer trails occur at the right. Some of the trails were worn much deeper than others. The accompanying diagram (Fig. 19) shows the dominant vegetation of each of these trails. Trails 1 and 2 are still in use and trail 1 shows no vegetation. Trail 3 is used occasionally. Trails 2 to 8

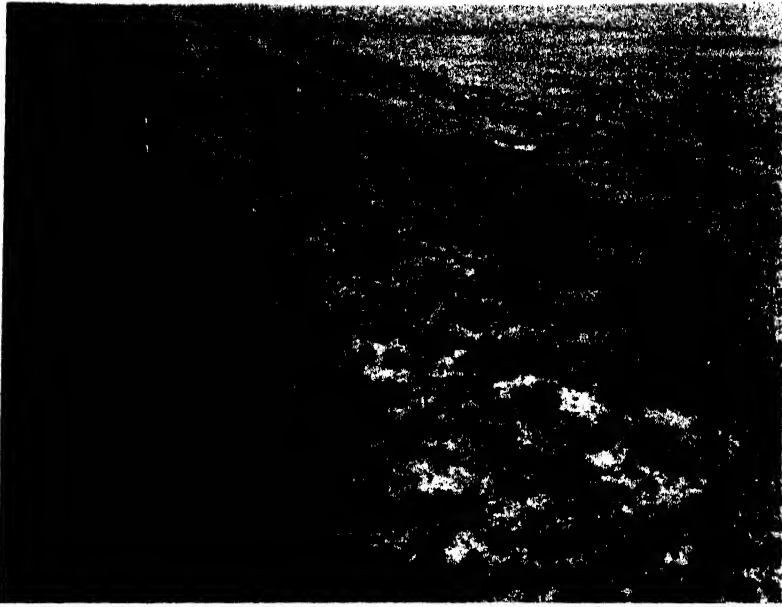


Fig. 11. Road in use in 1897 and abandoned about 1904. Vegetation nine years old when photographed. Central portion dominated by *Munroa squarrosa* and *Schedonnardus paniculatus*, while both sides are dominated by *Buchloë dactyloides*, the runners of which have moved in from the sides. *Gutierrezia sarothrae* and *Aristida longiseta* have established themselves in the central part of the road in the background. Moisture conditions at this point were favourable and *Buchloë* showed unusual activity in advancing on to the road. Road at right consisted of but a single wagon track. Photographed Sept. 17, 1914.

are partially covered with *Polygonum*; 9 and 10 with *Polygonum* and *Schedonnardus*; 11 to 13 with *Gutierrezia*, *Schedonnardus* and *Buchloë*; 15, 17 and 19 with *Gutierrezia*, *Buchloë*, and *Schedonnardus*; 14, 16 and 18 with *Buchloë*, *Gutierrezia* and *Schedonnardus*; 20 with *Buchloë* and *Gutierrezia*, and 21 to 23 with *Buchloë* and *Bouteloua*. The revegetation of trails, which seldom exceed $1\frac{1}{2}$ feet in breadth, is more rapid than on roads 6 feet in breadth. The same stages are evident, however, in the succession. Revegetation of trails by *Buchloë* is accomplished largely by the runners. On the roads reseeding becomes an important factor.

A bare cattle trail with no remnant of vegetation of any kind is shown at the left of Fig. 18. Fig. 20 illustrates a trail abandoned about five years and now in the *Gutierrezia* stage, with *Schedonnardus* a remnant of the earlier stage and *Buchloë* becoming established slowly. Fig. 21 shows an old trail in the final stage of revegetation. The trail leads from the lower right foreground of the photograph back through the right central portion. It is distinguished with difficulty since there is no change of vegetation type and only the slight depression to mark its course.

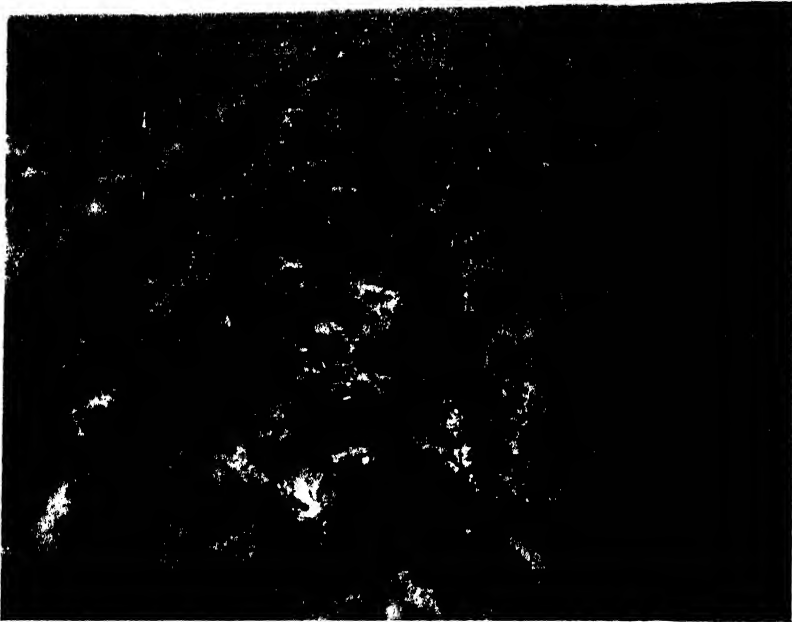


FIG. 12. Road formed about 1890 and abandoned in 1900. Vegetation thirteen years old. This road shows the *Gutierrezia* stage with the *Schedonnardus* stage represented by an occasional plant. Photographed Sept. 15, 1913.

The method of road formation and the different stages of succession are well illustrated in a single series of roads leading into the city of Akron, Colorado, from the east.

The first road was formed in 1886. During the next seven years two new tracks were formed on the south side of this road (Figs. 3, 4, 7). In 1893 a fence was constructed which shut off the road and forced travel to pass about 75 metres to the south. Here a new road was formed in 1893. Additional roads were formed and in 1913 nine roads paralleled each other at this place. Since 1913 one new track has been formed and the two roads in use in 1913 abandoned. There are now (1915) thirteen roads in all, the oldest having been formed in 1886 and the newest in 1914.

Revegetation on these roads is clearly shown in the bisect and transect

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in Fig. 23. Roads of various ages are here shown in one location and the succession on these abandoned roads is typical for this part of the Great Plains. The transect was made in 1913 and consequently does not apply to the vegetation shown in Fig. 3, which was taken two years later.

The vegetation at this point is typical short-grass. In road No. 1 the vegetation has been worn off (Figs. 4, 17), only the roots of the short-grasses remaining. An occasional trampled plant of *Polygonum aviculare* constitutes the only vegetation. Between roads 1 and 2 there is a narrow strip of undisturbed short-grass. Road 2 was abandoned early in the summer of 1913. Vegetation is almost as sparse as in road 1 and consists of the



FIG. 13. Same road as shown in Fig. 9. Although of the same age the vegetation here represents a somewhat later stage—a late *Gutierrezia* and early *Buchloë* stage. Photographed Sept. 15, 1913.

same species. Road 3 has been abandoned about one year and is covered with a fairly even growth of *Polygonum aviculare*. In this road an occasional plant of *Salsola pestifer* or *Gutierrezia sarothrae* is found. Road 4, abandoned about two years, is still in the weed stage and is dominated by *Polygonum aviculare*, with occasional plants of *Grindelia*, *Schedonnardus* and *Gutierrezia*. Between roads 4 and 5 the short-grass is left only in occasional mats. Road 5, abandoned about five years, is dominated by *Schedonnardus paniculatus*. With this are found many plants of *Gutierrezia*. No short-grass area separates road 5 from road 6. In the latter road, which has been abandoned about eight years, *Gutierrezia* is dominant, although *Schedonnardus* is still a

prominent plant. *Buchloë* is pushing in rapidly from the sodded area between road 6 and road 7. The vegetation of road 7 (Fig. 5) is approximately eleven years old. *Gutierrezia* is dominant, although *Schedonnardus* has not given way entirely, and both *Buchloë* and *Bouteloua* are entering.

Gutierrezia is dying out rapidly in road 8 (Fig. 5) which has been abandoned about fourteen years. *Buchloë* has pushed far into the road from the sod areas at the sides and has also established mats by reseeding. In road 9

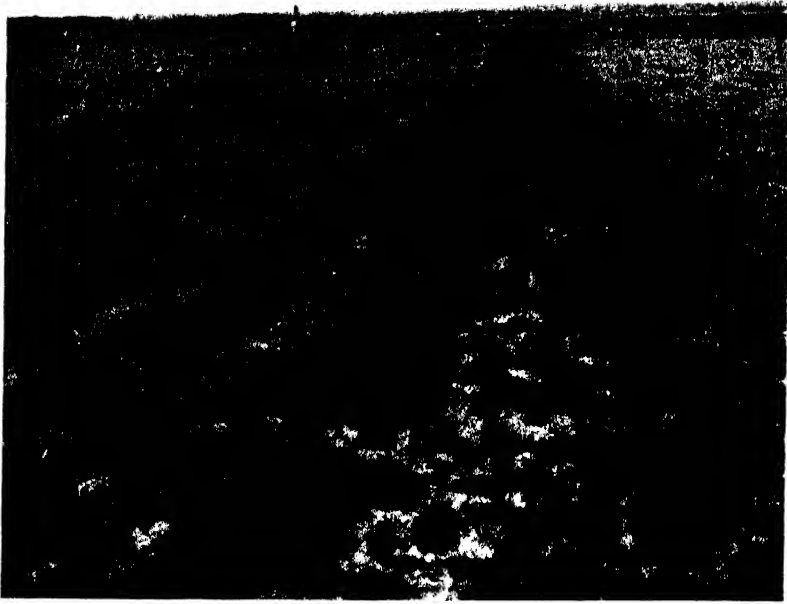


FIG. 14. Same road as shown in Figs. 11, 13. Here *Buchloë* is almost entirely established and a considerable amount of *Bouteloua* is also present at the left centre. At the right the *Gutierrezia* stage is still prominent. These three photographs illustrate the differences in stages which may be encountered on roads abandoned for the same number of years. Conditions for vegetation are not equally favourable. Just as in the native sod many places show a more primitive vegetation type, so in these roads such areas are usually clearly reflected in this secondary succession. In these three figures the stages of vegetation are youngest in the areas where the natural cover is most primitive in character and most advanced where the natural vegetation is of the purest type of Grama-Buffalo grass.

(Fig. 6), in which the vegetation is approximately seventeen years old, *Buchloë* has replaced *Gutierrezia*, except in an interrupted narrow strip near the centre of the road. Dead plants of *Gutierrezia* persist in the *Buchloë* sod.

In road 10 (Fig. 7) the vegetation is about twenty years old. Here *Buchloë* is dominant and most of the *Gutierrezia* plants are dead. Roads 10, 11 and 12 differ only slightly in vegetation. *Bouteloua* is a more important plant in road 12, which has been abandoned about twenty-three years, than in the later roads.

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Briefly, roads 2 and 3 belong to the (1) early weed stage, road 4 to the (2) late weed stage, road 5 to the (3) *Schedonnardus* stage, roads 6, 7 and 8 to the (4) *Gutierrezia* stage, and roads 9—12 to the (5) *Buchloë* stage.

The season 1915 was an unusually wet one and notes made on this series of roads on June 30 may be summarised as follows.

Native sod:—*Bouteloua gracilis* and *Buchloë dactyloides*, with a few scattered plants of *Plantago purshii*, *Festuca octoflora*, *Malvastrum coccineum*, *Grindelia squarrosa*, *Gutierrezia sarothrae* and *Erysimum asperum*.

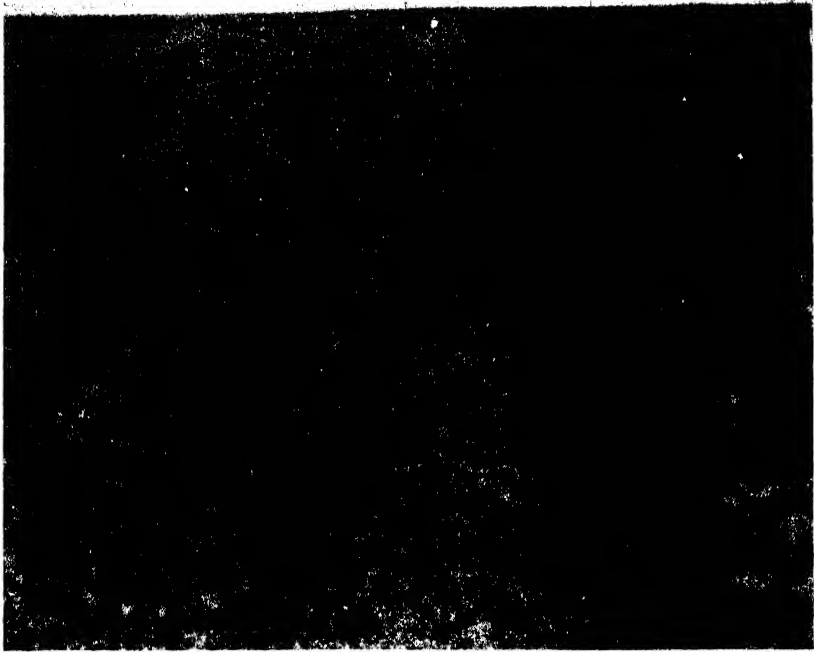


FIG. 15. Roads and trails formed in 1898 and soon abandoned. Vegetation about sixteen years old. All trails, except that at the extreme right, show the *Buchloë* stage. This trail, which has been used by cattle rather recently, is in the ruderal stage. The five tracks from the right to the left are the roads. Two trails are shown at the left.

Road 9:—pure *Buchloë dactyloides* at the sides; centre shows *Sitanion hystrix*, *Gutierrezia sarothrae*, *Grindelia squarrosa*, *Festuca octoflora*, *Plantago purshii*, *Malvastrum coccineum* and *Erigeron canus*.

Road 8:—rather open vegetation of *Buchloë dactyloides*, with scattered plants of *Gutierrezia sarothrae*, *Schedonnardus paniculatus*, *Grindelia squarrosa*, *Sitanion hystrix*, *Festuca octoflora*, *Plantago purshii*, *Erysimum asperum*, *Lepidium ramosissimum*, *Malvastrum coccineum*, *Hedeoma hispida* and *Psoralea tenuiflora*.

Road 7:—scattered growth of *Gutierrezia sarothrae* and *Schedonnardus paniculatus*, and a few plants of each of the species listed under road 8.

Road 6:—very open—scattered plants of *Gutierrezia sarothrae* and

Schedonnardus paniculatus and an occasional plant of *Grindelia squarrosa*, *Sitanion hystrix*, *Hedeoma hispida*, *Malvastrum coccineum* and *Sporobolus cryptandrus*.

Road 5:—more open than 6 and dominated by *Schedonnardus paniculatus*, with a few plants of *Sitanion hystrix*, *Gutierrezia sarothrae*, *Grindelia squarrosa*, *Lepidium ramosissimum*, *Plantago purshii*, *Verbena bracteosa* and *Buchloë dactyloides*.

Road 4:—largely *Polygonum aviculare*, with a few plants of *Schedonnardus paniculatus*, *Gutierrezia sarothrae*, *Festuca octoflora* and *Plantago purshii*.



FIG. 16. Road formed in 1891 and abandoned in 1892. Vegetation about twenty-one years old, and can be distinguished from the undisturbed sod only by lower level of the soil surface. Photographed Sept. 20, 1913.

Road 3:—*Polygonum aviculare*, with a small number of plants of *Schedonnardus paniculatus*, *Festuca octoflora*, *Sitanion hystrix* and *Gutierrezia sarothrae*.

Road 2:—a pure dense cover of *Polygonum aviculare*; this plant is much darker in colour in this road than in road 3, due to the better moisture supply; crude chlorophyll extract shows the chlorophyll content to be about three times as great as in road 3.

Road 1:—a few scattered plants of *Polygonum aviculare*.

Road 0:—bare except for an occasional plant of short-grass in the central portion of the road.

A comparison with the notes taken in 1913 shows very little change in the

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older roads but a more pronounced change in the younger roads. The change of vegetation in two years is slight. Road 1 has passed into the early weed stage, roads 2 and 3 into the late weed stage, while road 4 has almost passed from the weed stage to the *Schedonnardus* stage.

GENERAL DISCUSSION.

Although some variation is found in the revegetation of different roads in this region the following stages may be clearly distinguished.

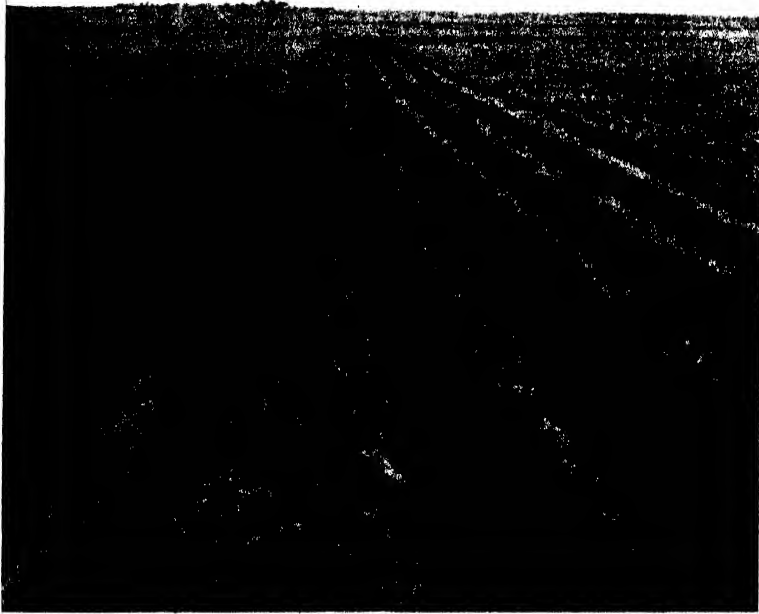


FIG. 17. Roads and trails. The third and fifth tracks from the left represent the oldest road. These tracks are now in the *Buchloë* stage. The second and fourth tracks are younger and show about half as much *Buchloë* as the oldest road. The first track at the left is a new cow trail and shows no vegetation. Another cow trail at the extreme right is in the *Buchloë* stage. The trails are only approximately parallel to the roads. Photographed Sept. 17, 1913.

The first, or early weed stage, formed on roads abandoned from one to three years. Plants are scattered, and in dry years are small. In wet years this stage passes rapidly over into the second stage. The species which constitute this stage are chiefly the following weeds:—*Polygonum aviculare*, *Salsola pestifer*, *Verbena bracteosa*. With these occur the following annuals or biennials which occur regularly in the short-grass sod:—*Plantago purshii*, *Festuca octoflora*, *Grindelia squarrosa*. A great deal of variation is shown, and any of the following may also occur:—*Dysodia papposa*, *Amaranthus blitoides*, *Amaranthus graecizans*, *Chenopodium incanum*.

The second, or late weed stage, on roads abandoned from two to five years, is one in which the plants which have entered in the first stage reach their greatest development and begin to disappear. In the latter part of this stage *Schedonnardus paniculatus*, *Gutierrezia sarothrae* and *Malvastrum coccineum* enter.

The third, or *Schedonnardus paniculatus* stage, extends from four to eight years after abandonment. *Schedonnardus* replaces the weeds which preceded and becomes dominant. *Gutierrezia sarothrae* gradually enters and becomes increasingly more important.

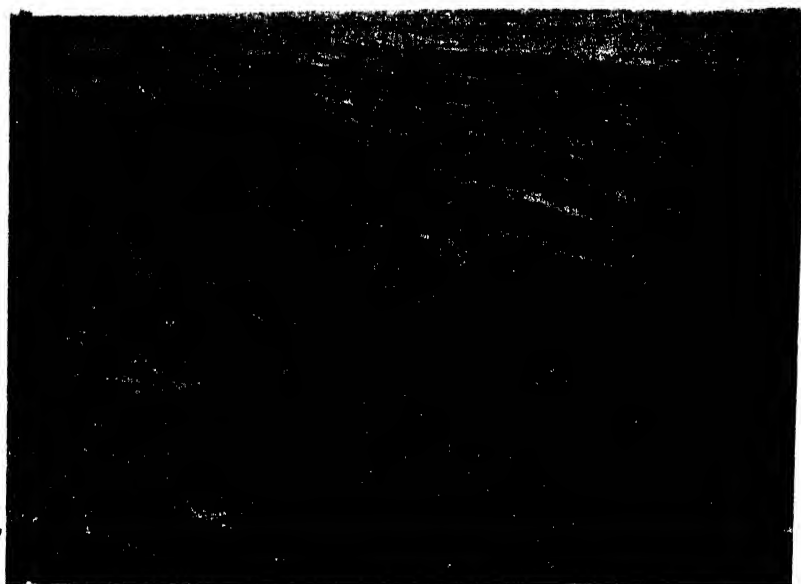


FIG. 18. A series of twenty-three trails and roads, the oldest at the left and the youngest at the right. Beginning at the right, trails 1 and 2 are still in use. Trail 3 is also used occasionally. Trails 2 to 8 are mostly bare but partly covered with *Polygonum*; trails 9 and 10 with *Polygonum* and *Schedonnardus*; 11, 12, and 13 with *Gutierrezia*, *Schedonnardus* and *Buchloë*; 15, 17 and 19 with *Gutierrezia*, *Buchloë* and *Schedonnardus*; 14, 16 and 18 with *Buchloë*, *Gutierrezia* and *Schedonnardus*; 20 with *Buchloë* and *Gutierrezia*, and 21 to 23 with *Buchloë* and *Bouteloua*. Trails 14 to 23 show dead *Gutierrezia* plants. These trails have been formed by both vehicles and cattle. Photographed Sept. 17, 1913.

The fourth, or *Gutierrezia sarothrae* stage, occurs on roads abandoned from seven to fourteen years. This plant gradually replaces *Schedonnardus* and is in turn replaced by *Buchloë*.

The fifth, or *Buchloë dactyloides* stage, occurs on roads abandoned from thirteen to twenty-three years. This plant gradually kills out most of the *Gutierrezia* but is never entirely replaced by any other. *Bouteloua* gradually enters and the typical short-grass sod formed in the next stage.

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The sixth, or *Bouteloua gracilis*—*Buchloë dactyloides* stage, extends from twenty to fifty years after abandonment. At the end of this time the composition of the vegetation cannot be distinguished from the undisturbed short-grass. Under unfavourable conditions the pure short-grass sod is never developed.

		ORDER OF IMPORTANCE.				
		1	2	3	4	5
TRAIL NUMBER	1*	O				
	2*	O	O	P		
	3†	O	O	O	P	
	4	O	P			
	5	O	P			
	6	O	P			
	7	O	P			
	8	O	P			
	9	O	P	S		
	10	O	P	B	S	
	11	O	O	G	S	B
	12	O	S	G	B	
	13	O	G	S	B	
	14	O	B	G	S	
	15	O	G	B	S	
	16	B	O	S	G	
	17	G	B	O	S	
	18	B	G	S		
	19	G	B	S		
	20	B	BG	G		
	21	B	BG			
	22	B	BG			
	23	B	BG			

* STILL IN USE.

† STILL USED OCCASIONALLY.

O = BARE GROUND

P = POLYGONUM AVICULARE

S = SCHEDONNARDUS PANICULATUS

G = GUTIERREZIA SAROTHRÆ

B = BUCHLOË DACTYLOIDES

BG = BOUTELOUA GRACILIS

FIG. 19. Diagram showing the dominant vegetation of each of the 23 trails shown in Fig. 18.

There are certain variations in the successions outlined above. In eastern Colorado *Sitanion hystrix* or *Munroa squarrosa* may occasionally

take the place of *Schedonnardus paniculatus*. Nearer the mountains *Dysodia papposa*¹ often initiates the weed stage. Under more favourable conditions, i.e. farther east, where the rainfall is greater, or on more sandy soil, *Aristida longiseta* will take the place of the *Gutierrezia* stage. Nearer the mountains in Colorado, in a vegetation dominated by *Bouteloua gracilis*, *Stipa vaseyi* takes the place of *Gutierrezia* and the vegetation passes directly into the *Bouteloua* stage from the *Stipa* stage, or through an intermediate stage of *Muehlenbergia gracillima*¹. Farther north *Artemisia frigida* takes the place

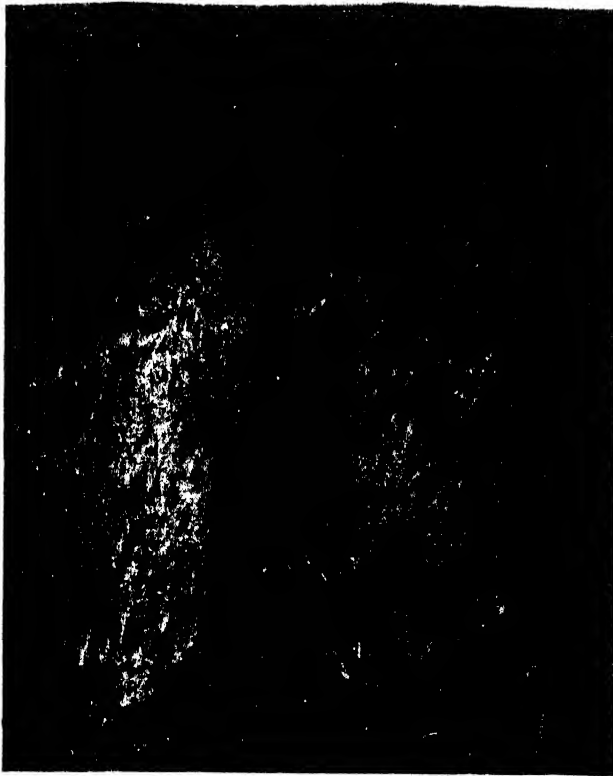


FIG. 20. Cattle trail abandoned about five years. Vegetation is in *Gutierrezia* stage. Some *Schedonnardus* still present and *Buchloë* entering. Photographed Sept. 20, 1913.

of *Gutierrezia* and is replaced by *Bouteloua gracilis*. In this case the fifth stage in the succession outlined below is omitted. In wheat grass (*Agropyron smithii*) areas this plant enters as the first perennial and is followed by *Buchloë* and *Bouteloua*.

¹ Shantz, H. L., "A Study of the Vegetation of the Mesa Region East of Pike's Peak. I. The *Bouteloua* Formation. II. Development of the Formation." *Botanical Gazette*, 42, 179—207, 1906, pp. 190—195.

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The succession as outlined here applies with almost no modification south to the "pan-handle" of Texas, and is typical, with minor modifications, for succession anywhere in the *Bouteloua*—*Buchloë* or *Bouteloua* associations from Texas to Montana. As modified by the discussion above the following is a general statement of the species which dominate the different stages:

(1) **Early weed stage:** scattered plants of:—*Polygonum aviculare*, or *Verbena bracteosa*, or *Salsola pestifer*, or *Dysodia papposa*, or *Amaranthus blitoides*.



FIG. 21. Old trail showing complete revegetation. Photographed Aug. 27, 1907, near Burlington, Colorado. (From Plate I, Fig. 1, Bulletin 201, Bureau of Plant Industry.)

(2) **Late weed stage:** dense growth of plants of stage (1).

(3) **Short-lived grass stage:** *Schedonnardus paniculatus*, or *Munroa squarrosa*, or *Sitanion hystrix*.

(4) **Perennial stage:** *Gutierrezia sarothrae*, or *Aristida longiseta*, or *Stipa vaseyi*, or *Artemisia frigida*.

(5) **Early short-grass stage:** *Buchloë dactyloides*, or *Muehlenbergia gracillima*.

(6) **Late short-grass stage:** *Bouteloua gracilis*—*Buchloë dactyloides*, or *Bouteloua gracilis*.

The stages of succession here outlined as they occur on abandoned roads do not differ essentially from those on fields which have been abandoned¹.

THE CAUSES OF THE SUCCESSIONS.

The successions are initiated by the destruction of the plant cover. Where a road is abandoned, the soil is generally well supplied with water and conditions are unusually favourable for plant growth. Any of the plants of the later stages of the succession would grow here, but those which are best adapted rapidly



FIG. 22. A graded roadway with road formed at the right of the centre. The grading was done two years before. The principal plants are *Polygonum aviculare*, *Salsola pestifer*, *Gaura coccinea*, *Malvastrum coccineum*, *Amaranthus retroflexus*, *Amaranthus blitoides*, *Chenopodium leptophyllum*, *Chenopodium album*, *Chenopodium incanum*, *Leptilon canadense*, *Buchloë dactyloides* and *Grindelia squarrosa*. The vegetation is much more mixed than on ungraded roads, and more nearly like that on abandoned tilled land. Photographed Aug. 23, 1915.

to seed the new area enter first. It is natural, therefore, that the first stage should be a weed stage. The density of the stand in the early weed stage is a measure of the success with which plants have seeded this area and germinated. In the late weed stage the density of stand and the amount of

¹ Shantz, H. L., "Natural Vegetation as an Indicator of the Capabilities of Land for Crop Production in the Great Plains area." U.S. Department of Agriculture, Bureau of Plant Industry, Bulletin 201, pp. 40—42.

42 *Plant Succession on Abandoned Roads in Eastern Colorado*

growth is an expression of the amount of water available for growth. In this second weed stage the area is often seeded so densely that the individual plant cannot develop, but remains small and stunted.

The next stage is a temporary grass stage usually formed by *Schedonnardus*. A glance at Fig. 9, will show how well this plant is adapted to reseed these abandoned roads. The depressions are often filled with the wiry panicles of this plant which is present in small numbers in the natural short-grass sod. The panicles are blown by the wind and lodge among the weeds on the old roads. Here when once established *Schedonnardus* shuts out the annuals, since a surface feeding perennial can usually exhaust the moisture supply in the surface soil before the young seedlings of the weeds can become established.

Schedonnardus, which is a short-lived perennial, does not replace the few plants of *Gutierrezia* which have already entered and does not prevent new plants from becoming established. *Gutierrezia* can utilize soil moisture of the deeper layers as well as the surface layers and gradually replaces the *Schedonnardus* which, although not an annual, is a comparatively short-lived grass.

The long-lived surface feeding *Buchloë* gradually replaces the *Gutierrezia*. By consuming the water as it enters the surface soil, *Buchloë* effectively cuts off the moisture supply to the deeper soil layers and the deep root system of *Gutierrezia* is no longer effective in supplying water to the plant. Much of the *Gutierrezia* gradually dies out and remains as dead bushes for some time. The roots can be detected in the soil under the *Buchloë* sod after the plants have disappeared from the surface. *Bouteloua* reseeds very slowly and only after a number of years has it become as dominant as the *Buchloë*.

REVIEW

PROFESSOR CLEMENTS ON PALECOLOGY

Professor Seward has contributed the following remarks on the sections on "Past Climates and Climaxes" and "Past Succession" in Prof. Clements's recent work on *Plant Succession* reviewed in this JOURNAL, 4, p. 198:—

In Prof. Clements's volume on Plant Succession about 160 pages are devoted to the subject of Paleocology, a science defined by the author as bearing the same relation to Palaeobotany as Ecology bears to Botany. It is assumed that the "operation of succession was essentially the same during the geological past as it is to-day," and Lyell's dictum that the present is the key to the past is accepted as a guiding principle. It is assumed that the "operation of climatic and topographical forces in moulding plant-life have been essentially the same throughout the various geological periods." Though to a large extent the student of ancient floras must necessarily apply knowledge gained in present circumstances, there are certain general considerations based on our knowledge of the geological record which suggest differences of importance. The late appearance of the present dominant class of flowering plants means that in pre-Angiosperm days the conditions governing the struggle for existence, including opportunities of rapid dispersal, must have been very different from those which were imposed by the addition of the flowering plants. Moreover there are no satisfactory grounds for believing that the amount of carbon dioxide in the atmosphere was not greater in the Carboniferous period than it is to-day; and though similar in kind to those now in operation there is reason to suspect that the forces of denudation and earth-movements were in former ages greater in intensity than in the later stages of earth-history. Prof. Clements speaks of the great changes induced by the glaciation of Devonian and Permian times as similar in effect to those of the Pleistocene Glacial epoch, but he does not state the evidence on which his reference to a Devonian glaciation and its effect on the vegetation is based. Several passages are quoted from the admirable text-book of Chamberlin and Salisbury and useful summaries are given of recent geological work on the lines laid down by Suess, whose book is not directly referred to. The characteristic floras of the three great eras, Paleophytic, Mesophytic, and Cenophytic, were clearly foreshadowed, as Chamberlin and Salisbury point out, before the beginning of each period.

In the section devoted to the Plant Record two new terms are proposed, *strate* and *stase*; the former is used, in a sense similar to that conveyed by the well-known word allocthonous, for plant remains deposited with sedimentary material at a distance from their place of origin. The term *stase* is applied to material, such as peat, preserved *in situ* or autocthonous in origin. Strates are derived from many sources and are therefore of little value as evidence of plant succession.

There is an interesting discussion of the connexion between earth-movements and changes in climate and vegetation. As geologists have shown, the records of the strata reveal a recurrence of deformation-cycles, periodic movements of land and water on a

large scale, and these must have affected climatic conditions, the circulation of currents, and other factors concerned in the distribution and composition of floras. Special attention is called to the work of Huntington and others on the more recent climatic changes, but the methods employed in their investigations are hardly applicable to the more remote geological periods. The various kinds of geological evidence that have any bearing on ancient climates are considered, but one wishes that the author had dealt more fully with such botanical evidence as is afforded by the petrified tissues of Palaeozoic plants. The relatively sudden appearance of a highly developed Devonian land flora is discussed and the inevitable conclusion is reached that land plants existed in one or more preceding eras. There must have been at least three previous land floras, so it is assumed; first Algae, then Liverworts and probably Mosses, and thirdly herbaceous fernworts, this being the essential order of succession in wet soils at the present day. Our knowledge of pre-Devonian land plants is practically nil and we are free to speculate on the nature of the vegetation which clothed the earlier Palaeozoic continents. Until actual specimens are found it is idle to reconstruct the floras. My own view is that the floras of Silurian and Cambrian periods reached a higher degree of development than is generally supposed.

Prof. Clements speaks of the accepted view of the uniformity of the Carboniferous vegetation and refutes it; but for many years the existence of two botanical provinces with different climatic conditions has been generally recognised. In his treatment of the different floras the author quotes lists of genera without critically considering their botanical position, and he makes no mention of several contributions by European writers which are of interest from the point of view of the value of fossil plants as indices of climate. *Nilssonia* is inadvertently included among the Conifers.

The subject which Prof. Clements has discussed is an exceedingly difficult one and hitherto it has been neglected by the majority of palaeobotanists; the problems are clearly stated and the well-written and thoughtful presentations of the principles of paleocology are very suggestive. What is needed is a critical summary of the voluminous palaeobotanical literature by a practised palaeobotanist with the assistance of the stimulating work of so experienced an ecologist as Prof. Clements.

A. C. SEWARD.

NOTICES OF PUBLICATIONS ON FOREIGN VEGETATION

Shreve, Forrest. "The Vegetation of a Desert Mountain Range as conditioned by Climatic Factors." Carnegie Institution of Washington, 1915. Pp. 112. 36 plates and map. 18 text-figures.

This work, which deals with the Santa Catalina mountains, 20 miles from Tucson, Arizona, is a most interesting and important contribution to our knowledge of the determination of vegetation by climatic factors. The region dealt with exhibits these relations with wonderful clearness and sharpness and the author's account is thorough and well-arranged.

The Santa Catalina mountains are a comparatively small isolated range, not much over 20 miles long, and of roughly triangular outline, with the highest summit, Mount Lemmon, about the centre of the triangle. They stand at the south-western terminus of a series of isolated elevations which stretch away from the southern edge of the Colorado plateau. This series of mountain ranges is separated by an extensive valley system from the southern part of the Rocky Mountains, but have a much closer connexion with the Mexican Cordillera, and these geographical relations are reflected in their vegetation and flora. The Santa Catalinas rise from the level of the surrounding Arizona desert (approximately 3000 feet in altitude) to an extreme height of 9150 feet. The southern face, to which the present investigation is practically confined, is built entirely of gneiss, which weathers readily, giving rise to a loam soil. The base of the mountains is surrounded by the characteristic *bajadas* or alluvial outwash slopes of straight and gently graded profile, which form almost the whole area of the intermontane valleys of Southern Arizona, and here occupy the Santa Cruz valley in which Tucson lies.

VEGETATION

The *bajadas* bear the characteristic (1) *Microphyll and Cactus vegetation of the Arizona Desert*, and this extends up the lower slopes of the mountains till an altitude of between 4000 and 5000 feet is reached, where (2) *Encinal (woodland of evergreen oaks)* begins. *Encinal* extends upwards to between 6000 and 7000 feet and is there replaced by (3) *pine forest* dominated by *Pinus arizonica* (a form of *P. ponderosa*, the western Yellow Pine). Finally (4) *fir and spruce forest* dominated by *Abies concolor*, *Pseudotsuga mucronata* and *Pinus strobiformis* occupies the northern slopes above 7500 feet. These four zones into which the vegetation falls are exceedingly well marked and sharply defined (see Fig. 1).

(1) The basal slopes of the mountains, between 3000 and 4000 feet, present nearly the same vegetation as the upper *bajadas*, the most highly developed type of desert vegetation to be found in Southern Arizona or Sonora, both as regards number of perennial species and number of individual perennial plants per unit area. Its characteristics are openness of stand, lowness of stature and commingling of diverse vegetation types. Largest and most conspicuous of the succulents is the giant cactus *Carnegiea gigantea*, which is here in its optimum habitat and very abundant. Of microphyllous trees, *Prosopis velutina*, *Acacia*

greggii, *Acacia paucispina* and the green-barked "palo verde" (*Parkinsonia microphylla*), are the most abundant. The evergreen *Covillea tridentata* is greatly outnumbered by the ocotillo, *Fouquieria splendens*, and a large number of less striking shrubs are common. Much branched arborescent opuntias up to 12 feet in height are accompanied by lower platopuntias, and the globular *Echinocactus wislizeni* attains a height of four feet. The

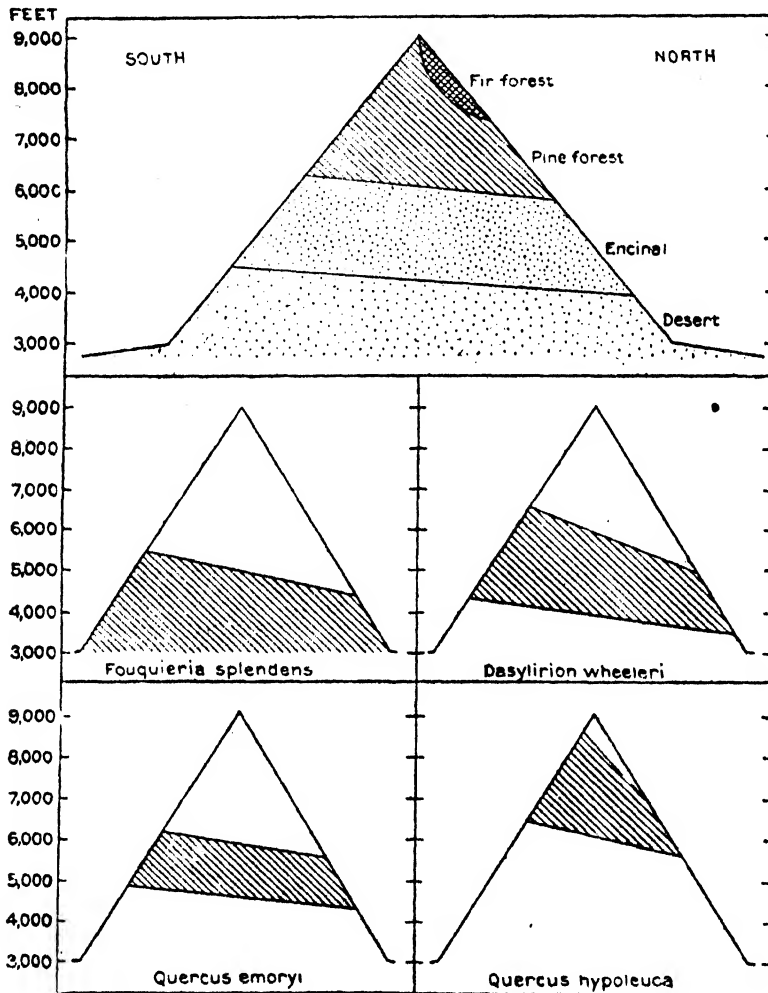


FIG. 1. Diagram showing vertical distribution of Desert, Encinal, Pine Forest, and Fir Forest in relation to slope exposure, together with diagrams showing effect of slope exposure on vertical distribution of *Fouquieria splendens*, *Dasylirion wheeleri*, *Quercus emoryi*, and *Quercus hypoleuca*.

seasonal rains both of winter and summer cause activity both of foliation and growth on the part of all the smaller shrubs, and these two widely separated seasons of rain bring forth wholly distinct sets of ephemerals. The latter may form a dense carpet on the ground in years in which the seasonal rains are well distributed and copious. The total flora of root perennials and ephemerals is large, and the relative abundance of the various

species fluctuates tremendously from place to place, and in the same spot it is by no means constant from year to year.

(2) *Encinal*. Between 4000 and 4500 feet the ecotone between desert and encinal is traversed. The characteristic bajada species are confined to southerly slopes and all but half a dozen find their uppermost limits. On the other hand characteristic encinal species like *Juniperus pachyphloea*, *Quercus oblongifolia* and *Q. arizonica* are found for the first time away from the cañons, and *Dasyllirion wheeleri* occurs in abundance on northerly slopes, together with the lowest individuals of *Nolina microcarpa*, *Arctostaphylos pungens* (manzanita), *Agave schottii* and *Yucca macrocarpa*. A much more complete ground cover than in the bajadas is afforded by the abundance of perennial grasses, root perennials and small shrubs.

The lower encinal has its commencement in the open orchard-like stands of *Quercus* on northerly slopes at about 4300 feet. At 5000 feet open encinal is found on all slopes except the steepest southerly ones, while on steep northern slopes it already forms nearly closed stands. The dense stands of the upper encinal begin to appear on southerly slopes at about 5800 feet and persist to about 6300 feet where large pines begin to dominate the physiognomy and true forest may be said to begin. The flowering and growth activities which are so conspicuous in the desert at the season of winter rains are very much reduced in the lower and are practically absent in the upper encinal. Leaves are retained by the evergreen oaks and the sclerophyllous shrubs throughout the winter, and are shed in April and May, simultaneously with the first growth of shoots, the renewal of foliage and the activity of the root perennials. This activity is commonly stopped by the advent of the arid fore-summer. In the upper encinal the early months of spring exhibit the rest period then obtaining in the forest region above.

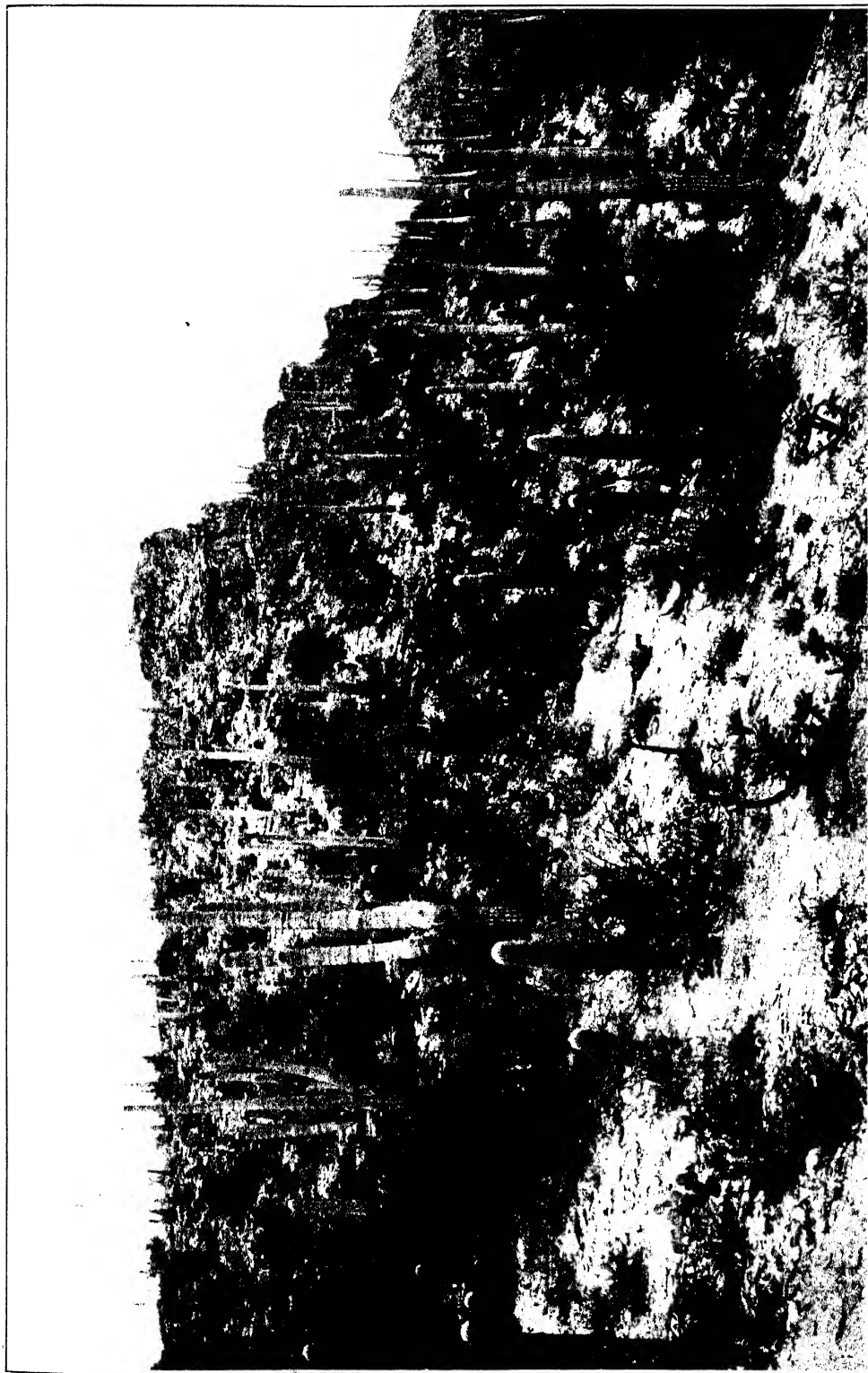
The encinal species of the desert-encinal ecotone have already been mentioned. With the exception of *Quercus oblongifolia*, which has a very narrow vertical range, rarely occurring above 5200 feet, all these are more abundant as we ascend and the number of species is augmented at about 5000 feet by the common trees *Quercus emoryi* and *Pinus cembroides* (one of the 'pignon' or 'nut' pines), as well as by various shrubs. The irregular carpet of low perennial plants, grasses, succulents and herbaceous species does much to lend character to the landscape, varying but little in density with the alternating seasons of vegetative activity and drought rest. The species of the upper encinal are much the same as those of the lower; the principal change being the increase in the density of stand. *Pinus cembroides* occurs in pure stands between 5300 and 6000 feet, and *P. chihuahuana* first appears at 5900 feet. The heaviest stands of the upper encinal are relatively dense thickets in which the trees are from 18 to 30 feet in height and so closely placed that it is very difficult for a horseman to make his way among them.

(3) *Pine forest*. One of the most striking changes encountered in traversing the vegetational zones of the Santa Catalinas is that from the closed and relatively low encinal to the open forest of *Pinus arizonica* with trees 50 to 60 feet in height. The lowest stands of pine possessing sufficient density to be regarded as forest occur on northerly slopes at 5800 to 6000 feet or on southerly slopes at 6000 to 6400 feet. The pine forest extends, on southern aspects, to the summit of Mount Lemmon, 9150 feet. It is not without vegetational features suggesting the effects of a climate not far removed from that of the desert. The openness of the lowest stands of *Pinus arizonica*, the high mortality among the pine seedlings, the character of the foliage of the shrubs and herbaceous perennials, and the deep-seated root systems of these plants, all point to the existence of a precarious soil-moisture supply and to atmospheric conditions conducive to active transpiration. The oaks characteristic of the closed forest are *Quercus reticulata* and *Q. hypoleuca*. The former is a low branching shrub which often forms thickets on the steep slopes of the

highest peaks, where it extends upwards to about 8600 feet. *Pseudotsuga mucronata* begins to occur on steep northerly slopes at 6100 feet and *Pinus strobiformis* (the Mexican white pine) at 6800 to 7000 feet. Deciduous trees characterise the streamways and flood plains at 6000 feet. *Platanus wrightii* is near its upper limit at this elevation, *Juglans rupestris*, *Prunus virens* and *Acer interior* are of frequent occurrence, while at 6500 to 6800 feet the lowest individuals of *Quercus submollis* and *Alnus acuminata* are met with. Throughout the pine forest are to be found a large number of herbaceous perennials, the great majority of which are characteristic of the dense stands of yellow pine though a few occur also in the upper encinal; and there is another large group confined to the close proximity of streams and streamways. The pine forest gives the impression of possessing a much richer flora of herbaceous plants than any other habitat on the mountains. In fact the list is not very large and the impression is due to a large number of the species being very common components of the vegetation. The low thorny shrub *Ceanothus fendleri* and the bunch-grass *Muhlenbergia virescens* are the most conspicuous plants in the open stretches among the pine forest. In the dense shade of the upper encinal *Pteris aquilina* var. *pubescens* is common, and again among the pines above 7500 feet, but it is infrequent in the lower pine forest.

(4) *Fir forest.* Between 7000 and 7400 feet there is a rapid change in the character of the forest stands on northerly slopes due to the increasing occurrence of *Pseudotsuga mucronata* and *Pinus strobiformis* and to the appearance of *Abies concolor*. Above 7500 feet *Pinus arizonica* becomes very infrequent on due northerly slopes. The *Pseudotsuga-Abies* forest is found in fine development at 7500 feet on steep north exposures and reaches its maximum development in size and stature of trees on the north slopes of Mount Lemmon at 8500 to 9100 feet. The vegetation of the fir forest presents a much more mesophytic aspect than that of the pine forest, being much more heavily and continuously shaded than the ground below the densest stands of yellow pine. The dense shade, the heavy litter and the high humus content of the soil tend to preserve its moisture throughout the arid fore-summer, so that the seedling trees and other plants of these situations are very far removed from the desiccating influences operative in the pine forest. The heaviest stands of *Abies* and *Pseudotsuga*, like most heavy coniferous forests, are relatively poor both in shrubs and herbaceous plants, and the ratio of the number of species to density of individuals is much greater than in the pine forest. Among the shrubs are *Jamesia americana*, *Symphoricarpos oreophilus*, *Ribes pinetorum*, *Rubus neomexicanus* and *Acer glabrum*: among herbs, *Bromus richardsonii*, *Cystopteris fragilis*, *Geranium coespitosum*, *Frasera speciosa*, *Thalictrum fendleri* var. *wrightii*, *Galium asperrimum*, *Viola canadensis* var. *rydbergii*, *Oxalis metcalfei*, *Fragaria ovalis*, etc. On the banks of constant and intermittent streams and on the narrow floodplains of the fir forest are to be found a great abundance and variety of trees and shrubs and the densest stands of herbaceous vegetation occurring on the mountains, including species of *Aconitum*, *Actaea*, *Delphinium*, *Viola*, *Hypericum*, *Geranium*, *Oxalis*, *Smilacina*, *Pyrola*, *Mimulus*, etc.

Geographical Derivation of the Flora. The desert species are derived from the two Mexican deserts lying east and west of the Sierra Madre, each of which has characteristic species of its own and also many in common. Perhaps 90 per cent. of the Southern Arizona species belong to these categories. On the other hand very few species range chiefly to the east, west or north, and of the few species distinctive of the Southern California and Mojave Deserts and of the Great Basin hardly any are represented in Southern Arizona. A large number of the Mexican species of the Santa Cruz valley range far southwards to Chile and many genera are represented in Argentina, Chile and even in tropical South America. The few genera of northern dominance or of transcontinental range are stream-side, palustrine or winter rain forms.



SANTA CATALINA MOUNTAINS, ARIZONA.
Lowest Desert Slopes, 2900 feet. *Carnegiea gigantea* (Giant Cactus), *Parkinsonia microphylla*, *Opuntia bigelowii*.



SANTA CATALINA MOUNTAINS, ARIZONA.

Open Encinal, 5200 to 5800 feet. Head of Soldier Cañon, looking north-east. *Quercus emoryi*, *Juncipus pachyphloea*, *Pinus ambrosoides*, *Arctostaphylos pungens*, etc. Note closed cirinal on north facing slope on the right above.

Reprinted from **Forrest Shreve**, "The Vegetation of a Desert Mountain Range," 1915, by the kindness of the author and of the Carnegie Institution of Washington.



SANTA CATALINA MOUNTAINS, ARIZONA.

Closed (Upper) Encinal on Manzanita Ridge, 5800 feet. Left *Pinus edulis* in flower. Centre *Quercus arborescens* in flower. Reprinted from **Forrest Shreve**, "The Vegetation of a Desert Mountain Range," 1915, by the kindness of the author and of the Carnegie Institution of Washington.



FIG. 1. Open Pine Forest, Steep South Slope of Main Ridge, facing south, 8500 feet.
Pinus arizonica, *Quercus reticulata* scrub.

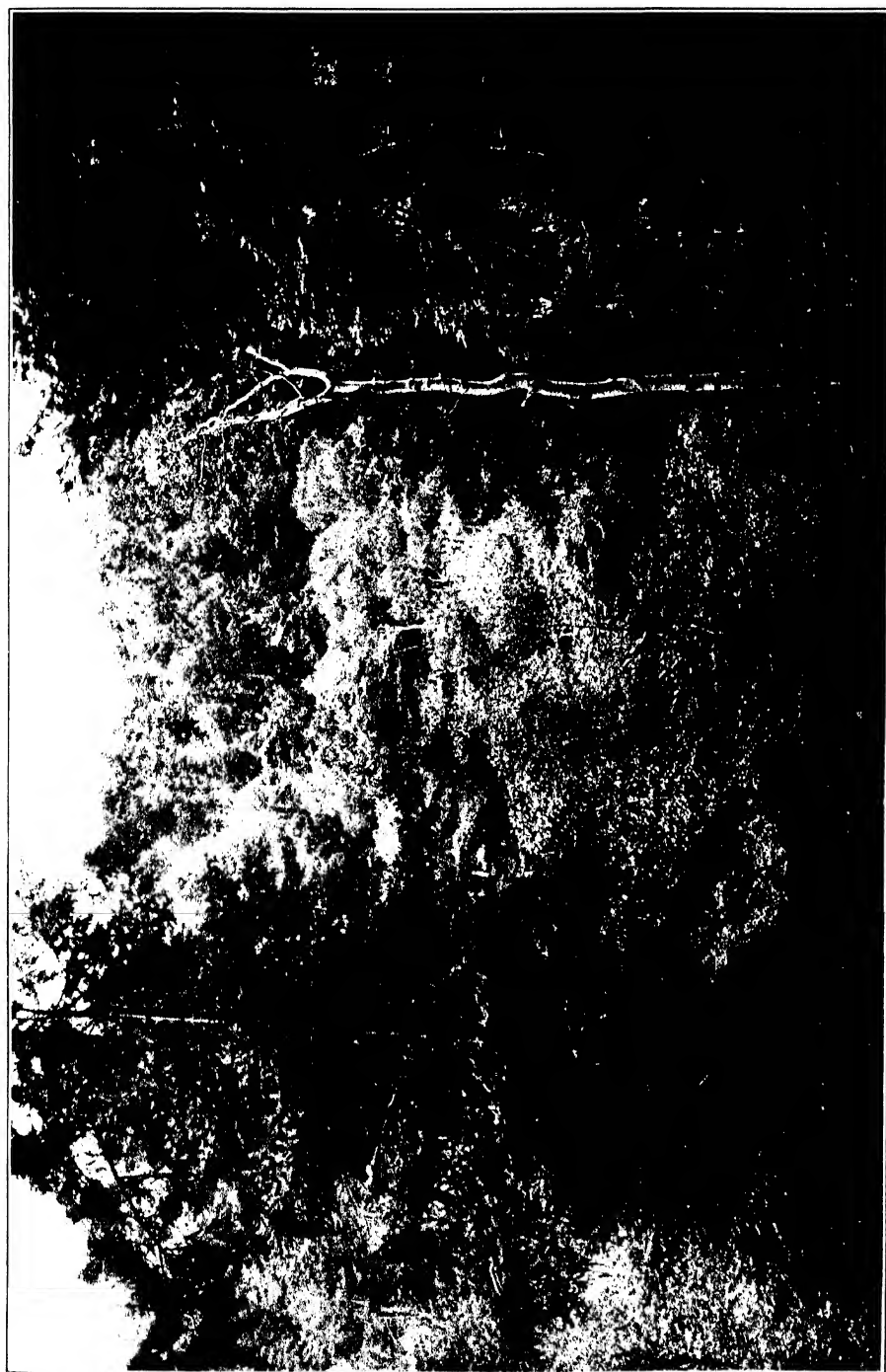


FIG. 2. Closed Pine Forest, Marshall Gulch, 7800 feet. *Pinus arizonica*.

SANTA CATALINA MOUNTAINS, ARIZONA.

Reprinted from **Forrest Shreve**, "The Vegetation of a Desert Mountain Range," 1917, by the kindness of the author and of the Carnegie Institution of Washington.

To face p. 48.



SANTA CATALINA MOUNTAINS, ARIZONA.

Canopy of Fir Forest on north face of Mount Lemmon, 8900 feet. *Pseudotsuga macrotecta*, *Abies concolor*, *Pinus strobiformis*.
 Reprinted from **Forrest Shreve**, "The Vegetation of a Desert Mountain Range," 1913, by the kindness of the author and of the Carnegie
 Institution of Washington.

The encinal vegetation is found throughout Southern Arizona and New Mexico at elevations of 5000 to 7000 feet extending throughout the mountainous parts of the Mexican states of Sonora, Sinaloa, Chihuahua and Zacatecas, and within the United States into Western Texas, Colorado and inner California. It is pre-eminently a community of evergreen oaks and pignon (nut) pines with many sclerophyllous shrubs. The dominant species of the Santa Catalina encinal are, like the desert species, of southern origin, the only northern element being Great Plains forms such as species of *Bouteloua* and a few belonging to the mountainous regions of Colorado, Utah and California.

The species of the forest flora, on the other hand, are largely northern, many forms being identical with Rocky Mountains species, while others belong to the Mexican Cordilleras. The former group is preponderant in number of species, while the latter is more conspicuous in the make-up of the vegetation. Of the northern forms some range across to the Atlantic coast, among which is *Achillea lanulosa*, scarcely separable from the cosmopolitan *A. millefolium*.

CLIMATE

The two leading climatic factors influencing the vegetation of the Santa Catalina Mountains are moisture and temperature. The former limits the downward distribution of forest and encinal, the latter the upward distribution of desert plants and perhaps of some encinal species. The two rainfall seasons last from December to March and from July to September respectively and the duration of the frostless period varies from 9½ months at Tucson to 4 months at the top of the mountains (see Fig. 2). The arid fore-summer (March to early July at the foot, June and early July at the summit) is the most trying time for plants since the soil moisture is low and transpiration active. The decrease in length of the arid fore-summer at the higher altitudes is accompanied by an amelioration of its physical conditions due to higher relative humidity and increased soil moisture. The humid mid-summer is the season of greatest vegetative activity; and at this time the moisture conditions of desert and mountain top are more alike than at any other season. The arid after-summer may show as extreme conditions as the fore-summer

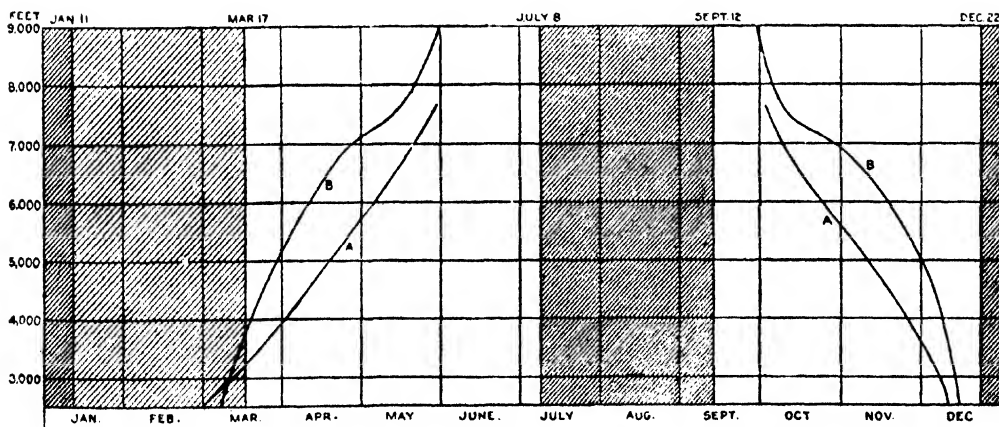


FIG. 2. Schematic representation of rainfall seasons and length of frostless season at Tucson and in the Santa Catalina Mountains, showing averaged limiting dates of rainfall seasons for 8 years and averaged limits of the frostless season for 1909, 1910, and 1911 (A A), and for 1912, 1913, and 1914 (B B).

but the duration of such conditions is shorter. A general cessation of vegetative activity occurs in September or October at the higher elevations and in October or November at the lower.

Rainfall. The annual rainfall at Tucson is about 5 to 8 inches in a dry year and 14 to 18 inches (24.7 inches were recorded in 1905) in a wet year. Precipitation increases as the mountains are ascended and the mean annual rainfall at 8000 feet is estimated at 35 inches. At Tucson about 50 per cent. of the yearly rain falls during the humid mid-summer season and about 30 per cent. during the winter rains. This percentage distribution is probably about the same on the mountains and the duration of the two wet seasons also approximately corresponds (see Fig. 2).

Soil Moisture. The most important aspect of this factor is the minimal soil-water contents occurring during the arid fore-summer. These vary from 1.0 to 5.5 per cent. of the dry weight of the soil up to an altitude of 6000 feet, and from 6.1 to 27.9 (fir forest) at 8000 and 9000 feet. The contrast between determinations made from soil taken on south and those taken on *north slopes* is, at the higher altitudes, very striking; and this corresponds with the distribution of vegetation. On the other hand the influence of *shade* in sustaining the moisture of soil during the arid seasons is so slight as to be negligible.

Evaporation and Atmospheric Humidity. The graphs showing the seasonal march of evaporation as determined by porous cup atmometers show a close approximation in groups, except at the beginning of the arid fore-summer, corresponding with the curves for 3000 and 4000 feet (desert), for 5000, 6000 and 7000 feet (encinal and lower forest edge) and for 8000 feet (heart of the forest), thus distinguishing very clearly the main vegetational zones. The graphs showing altitudinal decrease in evaporation in the arid fore-summer and the humid mid-summer respectively are pretty closely parallel, though the latter is slightly flatter, so that there is somewhat less differentiation in this respect between desert and forest during the damp than during the dry period. The rate of evaporation is about $3\frac{1}{2}$ times as great on the desert as at 8000 feet, and about half as great throughout the altitudinal zones in the humid mid-summer as in the arid mid-summer. The midday relative humidities in April, May and June in the desert are as low as 5 or 10 per cent., and these rise slowly through the late afternoon and more rapidly during the night to a daily maximum of 20 to 30 per cent. just before sunrise. The relative humidities of the forested region during the arid fore-summer may also be strikingly low. Thus at 7600 feet on May 20, 1911, the relative humidity at 11.30 a.m. and at 4.30 p.m. was 10 per cent., and at 9.15 a.m. on the following day 16 per cent. The highest humidity observed at this station was 48 per cent. at 4.30 p.m. on June 8, after the summit of the mountain had been covered for some hours with cumulus clouds. Similar results on a much larger basis of observation have been obtained by Pearson in the yellow pine forests near Flagstaff, Arizona. Thus desert humidity readings appear to be common in these desert mountain forests during the arid fore-summer. The lower evaporations observed at the higher altitudes are due to the nocturnal humidities, which are greater than in the desert, and to the more frequent cloudiness.

Temperature. A relatively small mountain mass, like the Santa Catalinas, in the midst of a desert plain, shows very different temperature conditions from those of extensive plateaus of the same elevation. The currents of warm air which ascend by day and the streams of cold air which descend by night¹ increase the diurnal ranges and give striking differences within very short distances. The differences of diurnal warming and nocturnal cooling which exist between the relatively bare soils of the desert and encinal on the one hand and those of the forest with its heavy cover of vegetation, litter of leaves and high humus

¹ **Forrest Shreve.** "Cold Air Drainage." *The Plant World*, 15, p. 110, 1912. See Notice in this JOURNAL, 1, 1913, p. 192.

content on the other are also considerable and tend to lessen the importance of topography at the higher elevations. The most striking instance of cold air drainage was met with at Bear Cañon, the floor of which (6000 feet) showed a minimum for the winter 1913-14 of 6° F. as compared with a minimum of 12° on the rim (7000 feet) and 18° on a ridge at 6000 feet. On the heavily forested upper part of the mountains however cold air drainage is very weakly shown, and this is due to the forest conditions above mentioned preventing the extremely intense radiation from the soil on which the rapid cooling at night giving rise to cold air drainage depends. The influence of cold air drainage on vegetation is seen chiefly in the shortening of the season of vegetative activity on the floor of a cañon as contrasted with its sides. Thus in the spring the foliage of the oaks on the floor of Bear Cañon is always well behind that of the oaks growing on the wall, and in the autumn the killing by frost of the herbaceous perennials and of the leaves of *Prunus*, *Populus* and *Rhus* takes place on the floor of the cañon at a time when the herbaceous plants of the slopes are still green and active. The occurrence of the highest individuals of every species on or near the summits of ridges and their invariable absence from the bottoms of cañons at the higher elevations are to be attributed to the absence of cold air drainage from the ridges and higher slopes together with other factors involved in slope exposure.

INFLUENCE OF TOPOGRAPHY

Slope exposure. The vertical distance between the upper and lower limits of a given species or a given vegetation is not widely different at the lower levels on north and south slopes respectively, and these limits differ on the two slopes by round about 1000 feet (see Fig. 1, p. 46). The difference however increases with altitude. In the desert and the lower encinal the upper limits of species differ by 600 to 1000 feet on the two exposures; in the forest by 1000 to 2000 feet. This effect is to be ascribed to increasing climatic differentiation between the two slopes as the altitude increases. Thus the ratio of evaporation to soil moisture on the north slope at 4000 feet is 33·1, on the south slope at 6000 feet 33·0; on the north slope at 6000 feet 16·0, and on the south slope at 8000 feet 3·9. The other important difference between north and south slopes is the higher soil and air temperature on the latter owing to increased insolation.

Streams and Flood plains. The streams and watercourses bring components of the upland vegetation of each altitude down along the streamways of the altitudes just below, so that the encinal is traversed by bands of forest and the desert by bands of encinal. Several striking examples of upland species occur in streamways much below their normal lowest occurrence on northern slopes. A depression of 1000 feet is common and one of 2000 feet occurs in a few cases but the plants do not develop into full-sized trees. The most extreme case is that of *Quercus hypoleuca* which occurs in the bed of a cañon 2700 feet below its lowest northern slope habitat. These depressions are due to the decrease of the ratio of evaporation to soil moisture owing to increase of soil moisture. That reduction of the ratio in this way may enable a plant to exist in air drier than that to which it is accustomed is shown by the survival of certain mountain plants at Tucson provided they are irrigated. Many mesophilous plants however cannot do this owing to their inability to pass on water to their transpiring systems as fast as it is withdrawn by the desert atmosphere.

Influence of ridges. Each of the leading types of vegetation in the Santa Catalina mountains reaches the uppermost limit of its occurrence on ridges and high south facing slopes, and the same is true of individual species. This phenomenon is distinct from the influence of streamways and of aspect. The extent by which the highest individuals on ridges exceed in altitude the highest individuals on south slopes is not normally more than

500 to 600 feet. The explanation is to be sought partly in the phenomena of cold air drainage which excludes the ascending species from the cañons, and partly from the extra insolation which the ridges obtain on winter days, since the upper limits of desert species are set by winter temperature conditions.

The author failed to find any evidence that competition between species in any way controls their distribution. He was impressed by the independence of each individual species in its climatic response, plants associated at any given altitude having very different limits to their ranges. Both these facts emphasise the *looseness* of the vegetation units of the desert and desert mountains. The conditions in such plant communities, where competition and the dependence of one species on another are practically absent, are very different from those obtaining in the more highly integrated plant communities of mesophytic vegetation. Since the limits of vertical range appear to have been very carefully worked out for a great number of Santa Catalina species it is to be regretted that the author has not published a statistical consideration of their correspondence with the limits of the vegetational zones.

Paulsen, Ove. "Some remarks on the Desert Vegetation of America." *The Plant World*, **18**, 1915, 155-161.

The author notes that the climatic zonation of vegetation in travelling from east to west in the United States (omitting the Rocky Mountains) represented by beech, oak, prairies, plains, sage brush, is paralleled by the zonation met with in travelling eastwards through Russia to Transcaspiæ: beech, oak, steppes, *Artemisia* plains, desert. The American deserts are not so barren and desolate as those of inner Asia but the vegetation at Mecca, California, comes near to the latter. A comparison of plains, sage brush and desert regions of N. America by means of Raunkiaer's spectra of life forms shows that Akron, Colorado (plains = steppe) and Tooele (sage brush) have marked maxima of *hemicryptophytes* and Tooele has a secondary maximum of *chamaephytes*, while Tucson, Salton Sink and Death Valley (deserts) have equally marked maxima of *therophytes*, the two last having secondary maxima of *phanerophytes*. With decrease of precipitation, therefore, there is a passage from *hemicryptophytes*, to some extent through *chamaephytes*, to *therophytes* and partly *phanerophytes*. In the passage from Southern Russia to Transcaspiæ there is a parallel transition, though the *chamaephyte* region, which may perhaps be represented by the *Artemisia* zone, is undetermined.

Pallis, Marietta. "The Structure and History of *Plav*: the Floating Fen of the Delta of the Danube." *Linn. Soc. Journ. Bot.*, **43**, 1916, 233-290, plates 11-25.

Plav, the floating fen of the Danube delta, is composed almost entirely of living reed, *Phragmites communis* β *flavescens*. The word is Russian and means 'floating thing' or 'floating stuff.' In Rumania *Plav* is practically confined to the Danube delta where its distribution is wide though sporadic. It consists of a compact raft-like structure from 8 cm. to 2 metres in thickness, composed of the interlaced rhizomes of the reed closely bound together by numerous roots, which retain much soil and thus completely fill the interstices between the rhizomes. The general surface projects about 4 cm. above the surface of the water and the thicket of reeds composed of the aerial continuations of the rhizomes rises vertically to a height (in the case of the flower-bearing extremities) of 5.15 m. or even 7.15 m. The individual *Plav* areas are not large though exact measurements are wanting. The reed of the Danube delta (*β flavescens*) differs from the type

of *Phragmites communis* in its larger size, the colour of its glumes and the greater frequency of buds on the nodes of the aerial shoots. The general habit of growth is closely similar. The rhizome of the reed is perennial and lives under water. It branches sympodially, the growing point turning upwards and often branching in the vertical direction. In deep water this vertical branching is abundant because the buds in the axils of the sheathing scales and also at the nodes of the bases of the aerial shoots develop if immersed. Thus huge stools are formed consisting of numerous vertical branches often compound to the sixth degree. The stool form of reed also occurs in the East Norfolk broads. In shallow water on the other hand the reed branches chiefly in the horizontal plane. In either case it fills up the space under water more or less completely. Each succeeding vertical rhizome branch is on the whole somewhat thinner and shorter than its parent, the finest and longest stems being those arising from the most basal (least compound) of existing rhizomes.

There are three growth stages of the reed—corresponding with open reed swamp, closed reed swamp and, in deep waters, Plav. Open reed swamp passes into closed reed swamp, by the filling up of the space colonised by the reed, and this into Plav. The last change occurs by detachment of the tussock from the bottom on which it is growing, first because of the death of the basal rhizomes and secondly because the water which circulates freely through the loose rhizomes below exerts pressure against the much branched solid upper portions of the stools so as to increase the pull on the rooted portion below. Floods and storms facilitate the process, which however seems to take place in any case at a more or less definite stage of development of the reed provided the water is deep. Plav is practically confined to the delta and its absence elsewhere is attributed to the magnitude of the floods carrying a large amount of fine inorganic silt, the deposition of which plants the reed afresh however insecure it may have become through the processes of its growth. No Plav is formed in the Norfolk Broads because the water is too shallow, the reed filling up the whole space from the bottom to the surface before decomposition of the base becomes general. In other words decay does not set in in the swamp stage but in the fen stage. Plav, when newly detached, does not differ from closed reed swamp except in that it floats, and this is not obvious to the eye. *Polystichum Thelypteris* is subdominant in this stage. Later the soil becomes darker and thicker as it is increased by the accompanying plants, of which *Typha angustata* and *Cladium Mariscus* are locally dominant, *Carex riparia* and *Polystichum Thelypteris* locally subdominant: 34 other species are recorded, including two willows (occasional), *Populus alba* (very rare), and three species of *Hypnum* (local). *Typha angustata* competes successfully with the reed (as does *T. angustifolia* in the Norfolk Broads) though it appears only to inhibit the reed's growth for a time. The next stage of the succession is strikingly similar in the East Anglian fen and in Plav. *Cladium Mariscus* becomes dominant, or alternatively a mixed sedge fen, with many of the same species, appears. The subsequent stages are very different owing to the difference of climate. In East Anglia *Juncus obtusiflorus*-fen, *Molinia coerulea*-fen or carr (forest of *Alnus glutinosa* etc.) follows: in Rumania after the tall dominants have disappeared the steppe climate begins to control the vegetation and salt marsh plants (*Salicornia herbacea* forma *stricta*, *Suaeda maritima*, *Aster Tripolium* etc.) appear on the Plav.

The vertical shoots of *Phragmites* in Plav vary strikingly in size. Each 'thicket' is composed of shoots more or less of one size, and the smaller and slenderer type of shoot is regarded as the aged form, each succeeding vertical branch being somewhat shorter and thinner than its parent. This change is regarded by the author as due to senescence of the plant, the 'major individual' of which is considered to be the whole series of shoots produced from the seedling up to death by senescence.

THE BRITISH ECOLOGICAL SOCIETY

ANNUAL GENERAL MEETING. DECEMBER, 1916

The Ninth General Meeting (Third Annual Meeting) of the Society was held on December 16, 1916, in the Botanical Lecture Room, University College, London, at 10.30 a.m. The chair was occupied by the President, Prof. F. W. Oliver, F.R.S. The minutes of the last General Meeting were read and confirmed and the reports of the Secretary and Treasurer were adopted. A statement of accounts for 1915 appears on p. 55.

In presenting the Accounts for 1915 the Treasurer reported that the liabilities shown had now been discharged and that the deficit which had been incurred in the first year of the Society, mostly in connection with giving the *Journal of Ecology* a good start, was gradually being reduced. The expenditure had quite justified itself and was now being recouped, the sales of the JOURNAL for the current year, 1916, being higher than for 1915, in spite of the times being adverse and some Continental subscriptions being held over in consequence of the War. The Auditor's certificate covered the Accounts since the beginning of the Society. On the motion of the Chairman the Accounts were adopted and passed unanimously.

In commenting upon the Treasurer's report the President announced that the accounts of the Society had been audited to December 31, 1915, in an extremely thorough manner, and the auditor had paid a high tribute to the ability of the Treasurer in conducting the finances of the Society.

On the proposition of Mr Watt a hearty vote of thanks was accorded to the auditor, whose services were gratuitous. On the proposition of Mr Wilmott, seconded by Mr Ramsbottom, a resolution was passed abrogating Rule 17 for the purposes of the present meeting.

A ballot was taken for filling the vacancies caused by the retiring Officers and Council Members, for which Miss Halket and Mr Wilmott acted as scrutineers. The Council's nominees, viz.: *Vice-Presidents*, Professor Weiss and Mr Tansley (Dr W. G. Smith retiring); *Council Members*, Dr S. M. Baker and Mr J. Ramsbottom (Messrs R. Lloyd Praeger and W. G. Smith retiring) were duly elected.

RETIREMENT OF SECRETARY

The President then announced that the Society was about to lose the services of the present Secretary and Editor, and proposed from the chair the following resolution, which was carried by acclamation.

"That the thanks of this Society be accorded to Dr Cavers on his relinquishing the positions of Secretary and Editor which he has occupied since its foundation. In particular he has furnished a number of incomparable reviews which have been a prominent feature of the JOURNAL and as Secretary he did much at the formation of the Society to secure its initial success."

Mr Tansley spoke in support of the motion, giving an account of what Dr Cavers had done during the period of the Society's inception, and proposed that Dr Cavers be elected an Honorary Life Member of the Society. This motion was seconded by Dr Salisbury and carried unanimously.

INCOME AND EXPENDITURE FOR THE YEAR 1915

<i>Income</i>		<i>Expenditure</i>	
	£ s. d.		£ s. d.
Subscriptions Received ...	117 6 0	<i>Journal of Ecology.</i> Cost of four parts including that published February, 1916, and distribution, etc. ...	221 13 11
Subscriptions in arrears, say ...	6 6 0	Secretary and Editor—Honorarium ...	25 0 0
Donations from Members of Council ...		Postages and Sundries—Secretary ...	6 3 3
British Vegetation Committee Account.		Balance—Surplus on the year, carried to Balance Sheet below ...	6 18 1
Share of profits on sales of publications, to receive, say...			
<i>Journal of Ecology</i> , Sales ...	119 12 3		
	<u>£259 15 3</u>		<u>£259 15 3</u>

BALANCE SHEET AT 31st DECEMBER, 1915

<i>Liabilities</i>		<i>Assets</i>	
	£ s. d.		£ s. d.
<i>Journal of Ecology.</i> Balance due to Publishers ...	71 3 3	Cash at London, County and Westminster Bank ...	10 2 9
Treasurer's outpockets, 1913-15 ...	17 6	Arrears of Subscriptions—see above ...	6 6 0
		British Vegetation Committee—see above	6 0 0
		Balance—Deficiency brought forward from 31 December, 1914 ...	56 10 1
		Surplus on year 1915, as above ...	6 18 1
	<u>£72 0 9</u>		<u>49 12 0</u>
			<u>£72 0 9</u>

NOTE. The stock of the *Journal of Ecology* is a further asset more than ample to cover the deficiency shown above.

HUGH BOYD WATT,

Hon. Treasurer.

I have examined the Accounts for years 1913-14, 1914-15, and 1915-16 and certify the same to be a correct statement and that all vouchers are in accordance with receipts and payments shown therein.

14th December, 1916.

L. M. ALDER.

PRESIDENT'S ADDRESS

The President then delivered his Address and spoke as follows:

It falls to my lot to deliver an address to the members of the Ecological Society under conditions very different from those prevailing when my predecessor in office gave us his masterly survey of the field which the then newly founded Society was about to occupy.

THE WAR AND ITS EFFECTS ON THE SOCIETY

A state of active war with the world's leading military power is calculated very seriously to affect a Society like ours, and that in a variety of ways. That we should have to mourn serious losses is, I suppose, inevitable. It was the natural thing that our younger men, where physically qualified, should serve their country in the fighting line, and indeed there could be no better preparation for soldiering than the open air instinct and eye for ground which are the equipment of the field naturalist.

Whilst our hearts are saddened at the loss of lives, so full of promise as were those of Laidlaw, Marsh and Lee and of the even younger men, some of whom had hardly completed their University courses, we feel proud at the universal testimony to their skill and gallantry in leadership and the high regard in which they were held by their brother officers and men. Marsh was a very loyal and zealous member of this Society, who throughout his period of military training never failed to attend our meetings and go on our excursions. Indeed the last time many of us saw him was on one of these occasions. In this I am sure he set a fine example. For whoever would best do his duty to his country in however humble a degree in these times needs to preserve the serenity of his mind. By keeping alive our interest in Nature, as Marsh did, by active participation we keep our vision clear and unsullied; we cultivate a certain detachment of mind, we preserve the mechanism of a normal judgment which should help us neither to be too cast down nor too elated by fluctuations in the fortunes of war.

Another way in which we are importantly affected is by the swiftly reached determination that this country shall in the future be far more nearly self-supporting than in the recent past. Properly interpreted this means the expansion of our productive rural industries and depends ultimately on the growing of plants.

THE FIELD AND THE LABORATORY

Ecologists when they went forth to the field in search of their problems took a step inevitable in the development of botany. Our forefathers found the study of systematic botany all absorbing and great herbaria were assembled. In this country at the middle of last century the systematic and geographical investigation of plants became paramount and no botanist could get professional advancement other than through the systematic mill. Although those days of dominance are long past work in the systematic field was never more urgent than at the present time.

Then came the era when the erection of laboratories became the rule, an era from which we are hardly yet emerging. In these the structure of plants can be studied with all the modern conveniences and their processes investigated under controlled conditions. The anatomical laboratory when it had exhausted the descriptive aspect of anatomy and cytology found further justification. Cytology attached itself to the chariot wheels of genetics, whilst anatomy, largely inspired by the study of ancient plants derived from our incomparable petrifications, has been extensively used as a clue in tracing the pedigree of plants.

The physiological laboratory on the other hand has concerned itself with the analysis of mechanism of the great plant processes as such—the building up of organic matter, water requirements, transpiration and the osmotic phenomena, irritability and the transformations which accompany enzyme action. That was the second phase.

The ecologist, though often imperfectly equipped for his adventure, has migrated to the field to study what he believes to be the phenomena that matter; to the place, that is, where the real problems of plant life are to be discovered. To him the laboratory, though still quite essential, has become just the place where these problems are to find their ultimate solution. But he works under one very serious disadvantage which we ought somehow to mitigate whenever the opportunity offers. The handicap in question depends upon the artificial obstacles which our urbanised University system sets to escape to the country. A week-end here and a fortnight there stolen from the summer is insufficient for keeping continuous touch with ecological problems. If it is a question of a field experiment it is difficult to devise this to meet the conditions in advance. If a laboratory experiment needs change of design and adjustment over and over again before it achieves the desired result, how much more will not time be cut to waste from the difficulty of realising fully the field conditions from the distant base?

This can be illustrated by a definite and very simple case. Some years ago I wanted to determine the depth to which mobility of ground penetrated in a certain sandy tract overrun by the tide in connection with the establishment of seedling halophytes. For this purpose I designed a piece of apparatus consisting of a brass tube cut into numbered segments. These were threaded on a central rod and sunk vertically in the sand to a sufficient depth and the rod withdrawn. When the tide had risen and fallen I dug up the place to find that the tube sections all remained *in situ* and that the forces effective in re-arranging the units grains of sand to a considerable depth were quite inadequate to move the pieces of tube. This preliminary experiment shewed that I had gone to work the wrong way altogether and that what was wanted was a column of coloured sand which could be let down into a hole to a known depth and then measured up after a tide had passed over it. So we commandeered a certain pair of blue opal glass chimney piece ornaments from the hotel and these were pounded up in mortars by the whole party till there was a supply of powdered glass sufficiently close in size and specific gravity to undergo displacement under the same conditions as did the sand of the sea-shore. This blue sand was let down into holes and without further difficulty the required data were obtained. What I want to demonstrate is that miscalculations in advance is of the nature of things, that it is necessary to devise technique as you go along and that this is a time-consuming business.

NECESSITY FOR REORGANISATION OF PERIODS OF STUDY IN THE UNIVERSITY

If we believe the field to be the most obvious place in which to enter botany, then we want our classes of all kinds in the field. The first obstacle to this is distance, and even were that annihilated there is the general system which prevails in the College time-table—according to which it is arranged that a number of different subjects successively engage the attention of students in hourly units each day.

The first reform necessary is a concentration of the subject so as to occupy the whole or a sufficient portion of the summer term, and for this to be possible a reciprocal concentration in the other subjects is involved. Drastic readjustments of this kind are most difficult to accomplish, you have the deadweight of the traditional routine against you. It would be easier if we could persuade our zoological colleagues to join forces and camp out together at some mutually acceptable centre say from March to July. Unluckily the present day Zoologist, apart from bird and insect men, has no great inclination for the

field. Still if the idea is put about it may secure adherents, and certainly if restrictions to daily travel should be imposed in the near future as a war measure, it might become practical politics to put a whole class into billets, huts or tents. In that case it would be obligatory so to organise the catering, etc., that the total charges for a student should not exceed those incurred when living at home.

ECOLOGY AND RURAL ECONOMY

The advantages that would accrue from such a proposed system would extend beyond its nominal objective. More particularly would the attention of the rising generation be directed to the occupations of country life, including farming and forestry. These indeed form the natural hinterland of ecology. What are agriculture and forestry but experimental ecology of a somewhat specialised type? We have much to learn from these economic branches, which have produced and will continue to produce data of extreme value. The immediate impetus which both these branches will receive in consequence of the war, the evident necessity that the country must be more self-supporting in the future than in the past, should open out to the ecologist a congenial and useful field for his activities. The borderland, if any, is hard to detect. To take two papers published quite recently; what could be more ecological for instance than Mr STAPLEDON'S "Pasture Studies" and what more in the right lines of forestry than Dr SALISBURY'S papers on Oak-Hornbeam Woods now appearing in our JOURNAL?

Another department that should prove attractive to many, because it involves pioneer work, is that of the utilisation of waste lands of which this country possesses so considerable and varied an assortment.

On the occasion of a symposium dealing with this subject in Section K at Newcastle, I listened with the greatest interest to an account by our late Vice-president, Dr W. G. Smith, of the intricate and attractive problems presented by the Scottish heath-lands. On these areas the rival claims of sheep, grouse, deer, forestry and minor farming for the utilisation of the same districts make up a nexus of highly complex economic and social problems which is most bewildering. It was evident to an outsider that the first step towards a wise solution of the matter in the interests of the community as a whole depended on a full study of the life histories of the plants and animals concerned, such as ecologists are accustomed to carry out.

But before any real progress of the nature of a combined effort can be made in the development of our waste lands it is urgently necessary that an exhaustive inventory and survey should be prepared under a central directing authority. I am not thinking of them so much as potential areas for immediate exploitation for the production of food as of their after-war value when for long years this country must be burdened with debt the interest of which will have to be raised internally. If I don't misapprehend the coming economic position it will be obligatory on us to do all that we know to increase home production, whilst quite independent of this it is becoming more and more widely recognised that increased production of food and timber is required for the security of the country in certain contingencies. In this connection I am reminded of a saying by E. Dalgas, one of Denmark's famous dune and heath reclaimers, after the country had been deprived by the Prussians in 1864 of the Duchies of Schleswig and Holstein. Dalgas said "What we have lost externally can by reclamation be regained internally," and he set to work and proved the truth of his assertion.

The prospect of developments of this kind must appeal alike to our ecological instinct and patriotic spirit, and there will I am sure be many among us who will be glad to serve in such capacities as their training and inclinations indicate when the moment for action arrives.

In the course of an interesting discussion on Forestry following a lecture by Sir H. Stirling-Maxwell at Newcastle, Mr Middleton of the Board of Agriculture spoke of projected developments in this particular field in a way to create in the minds of ecologists the expectation that at no great distance of time opportunities of the kind just indicated would become available.

APPLICATION TO THE ECOLOGY OF MARITIME VEGETATION

Certainly in the particular field with which I am most familiar, that of maritime vegetation, I am astonished continually at the extent to which the facts of autecology and of synecology alike, as they accumulate, are applicable to economic ends. Thus in reclaiming land from tidal waters a certain maturity of the intake is desirable if the operation is to give satisfactory results. With experience of the successions it becomes obvious that critical stages exist at which by intervention the attainment of maturity can be materially expedited. One of the reasons why there is liability to prolonged pauses in shore vegetations (as in many other cases too) depends on the difficulty which natural agencies encounter in bringing seed to the place that is waiting for it. This difficulty is illustrated by the following example.

We have at Blakeney a large area comprising a number of acres of sterile, level, stabilised shingle recently vacated by the blowing away of a dune complex. This area is named "The Desert." For five years it remained true to its name, till in the autumn of 1912 (I think it was) came a high spring tide which just swilled over this great flat and no more, spreading everywhere fertilising drift together with an unlimited supply of seeds of *Statice binervosa*.

In due course these seeds germinated and established freely, with the result that every August now our quondam "desert" glows purple from afar. Now had this tide been a few inches higher or lower, or had it failed to coincide in the moment of its occurrence with the presence of stores of seed still viable, it might have been a century before our desert became purpled over.

"The little more and how much it is,
The little less and what worlds away."

Again, take the relation of sea plants to the fixing of mobile ground. It is the function of vegetation to stabilise a shifting environment. *Psamma* on the dunes: *Suaeda*, *Tamarisk* and others on shingle are outstanding exponents of this fundamental metier.

With a knowledge of how these plants propagate and establish it is perfectly easy to take control and gain the mastery over moving ground, to raise the level of the crest and protect the shore line from tidal flooding and erosion. In large degree such natural methods might supersede many of the costly constructions of the engineer, and by their cheapness in execution and upkeep should be applicable to many stretches of shore not valuable enough to justify the old extravagant methods.

These examples are given from my own experience to shew how the everyday data of the ecologist may be used to serve a definite economic end. And what applies to these modest problems will I am sure hold good for other cases. Ecologists will I believe do much to establish their subject in the general esteem if they are able to apply their knowledge or direct their work into what are called profitable channels, especially at a time when exploitation and improvement of our land have become a national need.

I remember once a Scottish lawyer who had come to know something of our visits to Erquy asking why we did such things and what we were going to get out of it? I explained that it was done for pleasure, to gratify our curiosity, that we were young and had to let off steam somehow. To which he replied "it were a pity I couldn't turn all that talent to something useful."

PHENOLOGY

A few weeks ago an enquiry was passed on from the Meteorological Office for an opinion as to whether there were any records in phenology that might with profit engage the attention of their trained observers. Personally I was inclined to think such a move premature at the present moment, as phenology had gone a little out of fashion but I promised to raise the matter so that others better qualified than I could give their view.

Phenology or phenomenology deals with the study of the relation of periodic critical happenings in plants and animals to climatic factors. The pushing of buds, the opening of flowers, the ripening of wheat, the first song of the nightingale and the migrations of birds are its regular subject-matter.

The investigation of these phenomena really belongs to the hinterland of ecology and might with advantage receive the attention of some of our country members, no doubt in cooperation. One of the great attractions of the studies of single species to which we were exhorted by my predecessor would be in connection with phenomena of this kind. Every species of plant differs from year to year in its vegetative luxuriance, the richness of its flowering and the output of seed; whilst annual plants and weeds fluctuate enormously in their relative frequency. Everyone knows how on rare occasions, once in twenty years perhaps, some quite common species of plant transcends all experience and makes an epoch in its history. I remember particularly the case of the gorse bushes at Erquy on the occasion of an Easter visit, many years ago, in company with Mr Tansley. Not only was every gorse bush transformed into a continuous mass of flowers so that the rigid branches were often bowed down to the ground, but the event was simultaneous throughout the countryside, and what was even more remarkable every bush a different shade of yellow.

At Blakeney too, and indeed anywhere, parallel phenomena are constantly to be seen. Our plants take turns at bumper years and one might properly name the years after *Silene maritima*, *Convolvulus Soldanella*, and the Horned poppy, just as some people name them after Derby winners.

It occurs to me that possibly we are too prone in our enthusiasm for habitat and topography to neglect a little the claims of climate. Well, perhaps on a convenient occasion some of our members may be disposed to raise the matter for discussion. I am sure it should be one of general interest.

In regard to the significance of the original point raised, we shall I think all agree in welcoming it as an indication of a readiness to modify meteorological routine in the sense of bringing it into closer touch with the requirements of biologists. In this connection it is rather significant that the U.S. Weather Bureau should be attached to the Department of Agriculture, whilst our office originated under the Board of Trade. However, I must not pursue this matter across the Atlantic, as I want to keep this address within bounds; besides, we have an attractive programme before us.

Mr Tansley moved a vote of thanks to the President for his valuable and inspiring Address, and this was carried by acclamation.

PAPERS

Mr Tansley then gave a brief account of the Western Coniferous Forests of the United States, and short papers were read by Miss E. J. FRY, on "Cryptogamic Pioneers of the Shales in the Aberystwyth District" and by Mr RAMSBOTTOM on "Methods of investigation on the Ecology of Fungi." Discussion followed each of the papers and votes of thanks were accorded the authors. After the meeting the members were entertained to tea in the Botanical Department by the kindness of the President.

SUMMER MEETING AT ROTHAMSTED

The next meeting of the Society will take place at the Rothamsted Experimental Station on Saturday, June 9, by kind permission of the Director, Dr E. J. Russell.

Members are asked to keep this date open, as the meeting will afford an opportunity of examining the experimental grass plots in their most striking phase. These constitute a series of ecological experiments of a unique character which have now been in progress for over half a century¹. Other features will be the laboratories, the arable fields, and the Broadbalk and Geescroft Wildernesses². A detailed programme of the meeting will be circulated in due course, and it is hoped that arrangements can be made for the communication of papers during the morning.

E. J. SALISBURY,
Acting Hon. Sec.

*COMMITTEE FOR THE DEVELOPMENT
OF REGIONAL SURVEY*

This Committee exists for the purpose of promoting the study of areas in relation to their human centres (village, town or city). Each survey begins with the geography of the area and leads to an investigation of the human settlement from its origins and throughout the successive stages of its growth. It includes every aspect of the area occupied or dominated by the community—topography, geology, vegetation, fauna, etc.—and may be defined as the study of the human community and its environment from the ecologist's standpoint.

The work of regional survey has been taken up during the past few years in several parts of Great Britain, and has been largely used to synthesise many branches of school work in the study of the area in which the school is situated.

The third conference organised by the Committee will be held at Newbury, Berks. from April 7th to April 14th, when it is hoped that a detailed study will be made of the town and region from as many standpoints as possible. The results of these studies will be correlated to supplement a Regional Survey of the Newbury neighbourhood already in process of making by the Grammar School, in the buildings of which the Conference will be held.

Dr M. C. Rayner, Lecturer in Botany at University College, Reading, and a member of Council of the British Ecological Society, will have the direction of the section of the Conference dealing with plant ecology.

Ecologists desiring to attend the Newbury Conference may obtain information as to lodgings, etc., from Miss E. E. Kemp, Local Hon. Sec., Kingsbridge Road, Newbury. Information on the work of the Committee may be obtained from the Hon. Sec., George Morris, Esq., Friends' School, Saffron Walden, Essex.

¹ It may interest members to refer to a short account of the grass plots written some years ago—*New Phytologist*, **3**, 1904, p. 172.

² See this JOURNAL, **3**, 1915, p. 193, for an account of the two wildernesses.

LIST OF MEMBERS (JANUARY 1ST, 1917)

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THE SALT MARSHES OF THE DOVEY ESTUARY.

BY R. H. YAPP, D. JOHNS AND O. T. JONES.

PART II. THE SALT MARSHES¹.

BY R. H. YAPP AND D. JOHNS.

(With Plates XII—XVI and thirteen Figures in the Text.)

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§ 1. GENERAL FEATURES AND SOIL CHARACTERS.

The distribution of salt marshes on the banks of the tidal waters of the Dovey and its tributaries is shown in Fig. 1. On these marshes two main types of vegetation can be distinguished (Pl. XII, Phot. 1 and 3). The first is a close, dwarf sward, extensively used and highly valued as pasturage for sheep. The sward is intersected by winding creeks or channels which ultimately communicate with the river. In addition, there are numerous shallow, basin-like depressions or "pans," devoid alike of drainage outlets

¹ Part I appeared in this JOURNAL, 4, 1916, p. 27.

and of vegetation (Pl. XII, Phot. 2, etc.). The second type of vegetation is taller, and consists mainly of the sea rush (*Juncus maritimus*). In Phot. 1 the association **Juncetum maritimi** occupies only a few isolated patches of ground, but in many parts of the area it is the dominant type of vegetation (see Fig. 1). As a rule the boundary between sward and **Juncetum** is sharply marked (Pl. XII, Phot. 3). The whole marsh is periodically inundated by salt water, but the more elevated parts are submerged during the highest spring tides only.

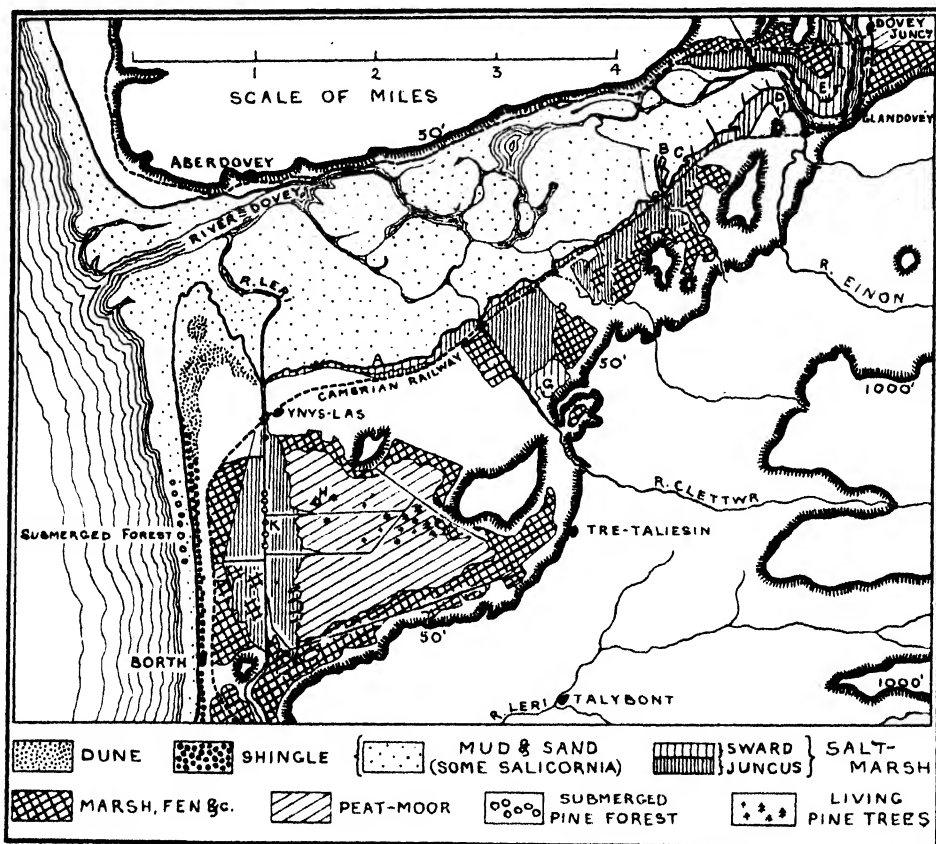


FIG. 1. Map showing present distribution of salt marsh and other natural vegetation on the Flats of the Dovey Valley. The thick lines, shaded on one side, indicate the 50-foot and 1000-foot contours.

Coastal or estuarine marshes of a similar character are well known in many other parts of the world, and considerable attention has been paid to them¹. Though no doubt the underlying problems are, in the main, fundamentally similar, salt marshes present many individual differences. At the present stage of ecological enquiry, therefore, it seems desirable that marshes in various localities should be described and compared. So far as British

¹ See Flahault et Combres (5), Ganong (6), Warming (23), Oliver (13, etc.), Ostensfeld (16), Harshberger (7), Massart (11), Johnson and York (9), and others.

salt marshes are concerned, the chief work hitherto done has been in Somerset¹ on the West Coast and Norfolk² on the East Coast.

In this paper, special attention is drawn to what may be called the *phyto-geological* problems presented by the Dovey salt marshes, and in particular, the origin and fate of the channels and "pans" mentioned above.

Soil Characters. In general, the marsh is developed on deep estuarine silt³, of a more sandy character than in many estuaries. At the surface the silt is more or less brown in colour, but below, it gradually changes to dark gray. In all parts of the estuary, the deposits contain sand mixed with finer sediments. The proportion of sand increases markedly as the mouth of the estuary is approached. Near Ynyslas (A, Fig. 1) a considerable amount of blown sand is found mingled with the river-borne deposits, especially along the northern edge of the marsh, adjoining the river bed. Blown sand also accumulates behind the free extremity of the large breakwater (B, Fig. 1). Elsewhere the finer sediments predominate, and the substratum may even assume in places the form of a tenacious mud. In certain parts, both along the Dovey and its tributaries, beds of peat underlie the silt⁴, and occasionally marsh halophytes may even be seen growing directly on old denuded peat surfaces.

A series of mechanical and chemical soil analyses had been planned, but time has not yet permitted these to be fully carried out. The following examples, however, will serve to illustrate the physical character of the soils towards the mouth of the estuary (at A, Fig. 1). The chemical analyses will be referred to later.

TABLE I. *Mechanical Analyses of Soils near Ynyslas*⁵.

Description of sample	Fine gravel	Coarse sand	Fine sand	Silt	Fine silt	Clay	Moisture	Loss on ignition	Approximate pore space
Armerietum									
Upper 4 inches	0.00	3.60	10.47	23.16	25.52	23.88	4.80	9.50	58 %
Second 4 "	0.00	13.53	14.61	16.35	23.86	20.98	3.15	7.36	56 %
Third 4 "	0.00	2.75	11.34	24.74	24.77	22.74	4.26	9.37	54 %
Lower Festucetum									
Upper 4 inches	0.00	43.00	24.70	18.36	5.85	0.85	1.15	5.50	46 %
Next 8 "	0.00	42.10	30.30	18.00	3.70	0.45	1.03	4.80	45 %

In this locality the **Festucetum** is developed mainly on a slightly raised strip of land along the northern or river edge of the marsh. Most of the blown sand is intercepted by this strip, hence the finer character of the soil of the **Armerietum**, which lies on its landward side. The probable effect

¹ Moss, (12, p. 17), Priestley (18).

² Oliver and Salisbury (15, p. 51), and other important Blakeney papers. Marsh (10).

³ Cf. Introduction, p. 29 (vol. 4).

⁴ See Introduction, Fig. 3, and pp. 28, 41, etc. (vol. 4).

⁵ Carried out according to the method adopted by the Agricultural Education Association (*Jour. Agric. Sci.* 1906, Vol. 1, p. 470). Each estimation was performed in duplicate, and the average taken. Cf. the analyses in Marsh (10, p. 91).

of the exceptionally sandy soil on the flora is dealt with later. Unfortunately no analyses are as yet available of soils further up the estuary, but their less sandy nature is unmistakable.

§ 2. THE PLANT ASSOCIATIONS OF THE SALT MARSH.

It is probable that few types of vegetation exhibit the effect of slight differences of level so distinctly as the halophilous plant-covering of a salt marsh¹. Thus arises the zonation described by various authors. The plant associations which occupy the respective altitudinal zones vary considerably in different marshes. Frequently, moreover, there are more or less marked differences in floristic composition, even within the same area, and at the same relative level.

In the salt marsh formation of the Dovey Estuary, five main zones of phanerogamic vegetation, each characterized by its own plant association, can usually be distinguished (see Fig. 2). These are:

5. **Juncetum maritimi** }
4. **Festucetum rubrae** } —highest,
3. **Armerietum maritimae**,
2. **Glycerietum maritimae**,
1. **Salicornietum europaeae** —lowest.

Associations 2, 3 and 4 constitute the sward alluded to in § 1. So far as salt marshes in other localities have been described, the succession of associations seen in the Dovey Estuary most nearly resembles that of the Severn marshes, also on the West Coast of Britain². The chief difference between these two areas is the presence of the **Armerietum** on the Dovey marshes, and its complete absence on the Severn³.

The chief constituent species of the five associations, together with their vertical ranges and approximate relative frequency, are diagrammatically represented in Fig. 2. A few notes may be added, first on the associations, and afterwards on the species composing them.

1. **Salicornietum europaeae**. An open association on bare silt (Pl. XIII, Phot. 8); often absent, especially towards the head of the estuary (it is not developed above B, Fig. 1).

2. **Glycerietum maritimae**. The lowest of the sward zones. Often nearly pure, but frequently dwarf, stunted *Salicornias*, and in the higher parts of the zone other plants, are associated with *Glyceria*. Except where the vegetation is rapidly extending on the surface of the silt, the **Glycerietum** occupies relatively little ground (Fig. 7 and Pl. XIII, Phot. 5 and 6). It is strictly a pioneer association, at first open, becoming closed later.

¹ But see Introduction, p. 38 (vol. 4).

² Priestley (18, p. 16).

³ Priestley (18, p. 17).

3. **Armerietum maritimae**. This often contains a number of species (Fig. 2), but *Armeria maritima* (= *Statice maritima*) is usually strongly dominant, sometimes occupying the ground to the practical exclusion of other species. In the lower parts of the zone, especially where badly drained, *Glyceria* is usually sub-dominant. Below this, the association merges imperceptibly into the *Glycerietum*, while at higher levels it passes into—

4. **Festucetum rubrae**. This is on the whole the most widely distributed of the sward associations. *Festuca rubra* is generally dominant, though other species may be sub-dominant or locally dominant. In many parts of the area, two fairly distinct sub-associations or societies can be distinguished, i.e.

(a) **Lower Festucetum**, with abundant *Armeria maritima*, which is usually sub-dominant. Its rosettes are larger than the “tillers” of *Festuca*, and when in full flower (May and June) it is the most conspicuous plant

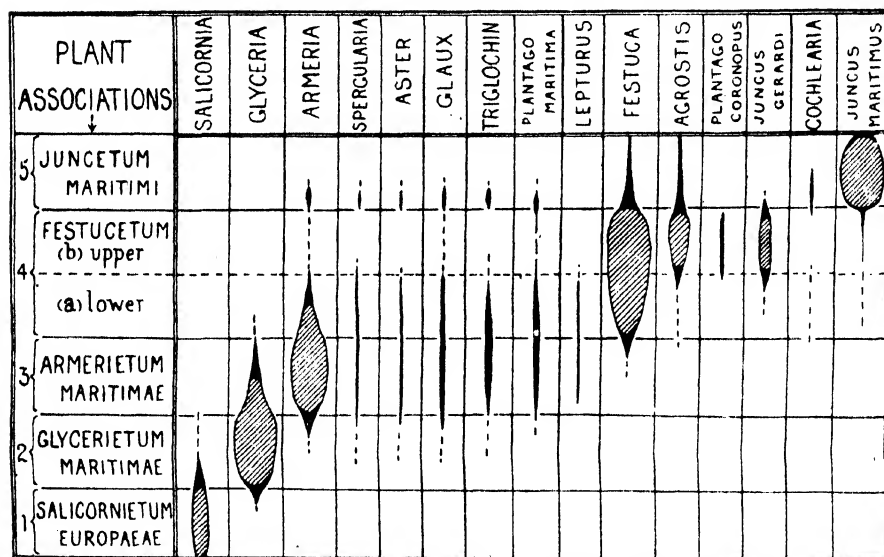


Fig. 2. Diagram showing approximate vertical ranges (not to scale) and average relative frequency of the various species. Dominant, sub-dominant and locally dominant species shaded, others black.

of this sub-association. A number of other species also occur both here and in the *Armerietum* (see Fig. 2), so that were it not for the numerical dominance of *Festuca rubra*, this lower sub-association might well be regarded as an upper sub-association of the **Armerietum**¹.

¹ The fact that *Armeria* is usually associated with either *Glyceria* or *Festuca*, together with a comparison of the Dovey and Severn marshes, gives the impression that in the Dovey area *Armeria* has been, as it were, superposed on the other associations; without, however, interfering to any great extent with the general succession. Indeed, the recognition of an **Armerietum** as an association distinct from the **Glycerietum** and **Festucetum** may be open to some objection. The reason for such distinction is that in the Dovey Estuary, not only is *Armeria* by far the most conspicuous of the sward plants, but also, at certain levels, one of the most abundant and characteristic.

(b) **Upper Festucetum**, with *Agrostis alba* var. *coarctata*, *Plantago Coronopus* and *Juncus Gerardi*. *Festuca* is dominant, but *Agrostis* and *Juncus Gerardi* are not infrequently either co-dominant or locally dominant. Near Glandovey, *Agrostis* is often dominant and very luxuriant at the highest levels. *Juncus Gerardi* and especially *Plantago Coronopus* are the most characteristic plants of this sub-association, for their vertical ranges are more restricted than those of the grasses¹.

5. **Juncetum maritimi**. The sea rush (*Juncus maritimus*) is dominant, and determines the general character of the vegetation. The relatively tall rushes (1.5–2.0 feet high) present a marked contrast to the dwarf herbage of the sward associations (Pl. XII, Phot. 3). *Festuca rubra* and *Agrostis alba* var. *coarctata* are abundant, and *Cochlearia officinalis* frequent. A striking characteristic of the lower parts of the **Juncetum** is the reappearance of a number of species of the **Armerietum** and **Lower Festucetum** zones, which are absent or rare in the **Upper Festucetum**; e.g. *Spergularia* (probably *S. media* Presl, = *S. marginata* Kit.), *Aster Tripolium*, *Triglochin maritimum*, etc. (see Fig. 2). The habit of these plants when growing among the rushes is far more luxuriant than on the sward, at least as regards their sub-aerial parts² (see Figs. 5 and 6). This is no doubt due partly to the shelter afforded by the rushes³, and partly to the close cropping of the sward plants by sheep.

The exact relation of the **Juncetum** to the **Festucetum** is somewhat puzzling, and has not yet been worked out. On the whole, the **Juncetum** occurs at a higher level, but this is not always the case. Occasionally the two associations are seen side by side, at the same level (see Table III), and apparently under the same conditions. Towards their upper limits both contain an increasing number of non-halophytic species. Thus, in the absence of *Juncus maritimus*, the **Festucetum** gradually passes over, as its level is raised, into alluvial pasture⁴. Similarly, on its landward side, where

¹ *Juncus Gerardi* on the whole descends lower than *Plantago Coronopus*; indeed in some other marshes it is especially characteristic of damper hollows at fairly high levels.

² When a species occurs in several different sward zones as well as in the **Juncetum**, the maximum size of the individuals is attained in the latter. There is, however, at least for some species, a particular sward zone where a secondary maximum is reached.

³ Cf. Yapp (24, p. 279). Evaporation measurements, extending over several days in August, 1914, showed that the average evaporating power of the air at the surface of the **Armerietum** sward was 2.26 times as great as in the **Juncetum** (at 3 inches above the ground, in a position sheltered by the tall rushes). But even the relatively exposed sward plants are to some extent sheltered by their position, i.e. by being close to the ground. Thus evaporation in the free air 6 feet 9 inches (= 206 cms.) above the ground was, on the average, 1.26 times as great as at the surface of the sward. One curious fact was brought out by the evaporation readings, i.e. that during the night periods (8 p.m. to 8 a.m.) evaporation was invariably slightly greater at the sward surface than in the free air 6 feet 9 inches above it. During the experiments the wind varied from calms to light breezes. Had a high wind prevailed, the differences would no doubt have been greater.

⁴ See Priestley (18, p. 18), and Moss (12, p. 20).

inundations by salt water are less frequent, the **Juncetum** either contains a large admixture of weeds, or, if the soil is wet, of fresh water marsh plants¹. E.g. near Glandovey, the following plants were found associated with *Juncus maritimus* in parts relatively remote from the influence of salt water: *Ænanthe Lachenalii*, *Molinia caerulea*, *Juncus conglomeratus*, *J. subnodulosus* (= *J. obtusiflorus*), *J. sylvaticus* (= *J. acutiflorus*), *Hydrocotyle vulgaris*, *Scabiosa succisa*, *Lychnis Flos-cuculi*, *Lotus corniculatus*, also *Potentilla Anserina* and other weeds.

Though it is usually possible to distinguish the five plant associations enumerated above, and though these are related in a striking manner to differences of level, yet the associations themselves are not always capable of rigid definition. This is especially true of the three sward associations, which as a rule shade gradually and often imperceptibly into one another, over a gently undulating surface. Indeed, we are really dealing with a number of species of plants, with different physiological requirements and capacities, and therefore with vertical ranges which differ not only in their positions with respect to tide levels, but also in extent². The different positions, or relative levels, occupied by these specific ranges, determine in general the associations; while their overlapping, together with differences in extent, gives rise to numerous transitional communities. Soil differences again may modify the vertical extent of the specific ranges, and so add further to the existing diversity.

Turf Analyses.

A number of quantitative analyses of the sward herbage were made according to the percentage frequency method. Pieces of turf 6 inches (= 15.25 cms.) square were cut out and carefully analysed. Instead of counting the entire individual plants (often difficult or impossible), each living shoot or branch appearing above the ground independently was regarded as a unit, and counted separately. For mixed, grassy vegetation of this kind, such a method of analysis affords a truer conception of the actual composition of the herbage than if entire plants were taken as units³. Individual plants vary greatly as regards both the number of "unit shoots" of which they are composed, and the amount of ground they cover. Thus a young *Armeria* plant may consist of a single shoot, while one fairly large old plant was found to possess 185 living rosettes, besides dead branches.

¹ Cf. Introduction, p. 39 (vol. 4), also Fig. 1 E.

² Cf. **Johnson and York** (9).

³ The method adopted was a slightly modified form of that used by **Armstrong** (1, p. 303) and **Stapledon** (20, pp. 132 et seq.). These authors counted entire individuals as far as possible, e.g. in the case of erect plants, but "each separate rooting of white clover and creeping grasses."

In most cases four or more typical samples were selected and analysed from each association, and averages taken. Samples were analysed from the sandy marsh near Ynyslas and from the more muddy marsh near Glandovey. The following results were obtained:

TABLE II. *Turf Analyses.*

	Ynyslas		Glandovey	
	No. of unit shoots in sample	Percentage frequency	No. of unit shoots in sample from 15 to up to 1036	Percentage frequency
Association 2: <i>Glycerietum</i>:				
<i>Glyceria maritima</i>	1428	99.8	1036	100
<i>Salicornia europaea</i> , agg.	2	0.1	—	—
Totals	1430	99.9	up to 1036	100
Association 3: <i>Armerietum</i>:				
<i>Armeria maritima</i>	470	61.6	523	88.0
<i>Glyceria maritima</i>	243	31.8	46	7.7
<i>Festuca rubra</i>	27	3.5	—	—
<i>Lepturus filiformis</i>	23	3.0	—	—
<i>Glaux maritima</i>	—	—	20	3.4
<i>Triglochin maritimum</i>	—	—	5	0.8
Totals	763	99.9	594	99.9
Association 4: <i>Festucetum</i>:				
(a) Lower , with <i>Armeria</i> ,				
<i>Festuca rubra</i>	862	85.5	528	68.0
<i>Armeria maritima</i>	104	10.3	236	30.4
<i>Juncus Gerardi</i>	24	2.4	1	0.1
<i>Lepturus filiformis</i>	14	1.4	—	—
<i>Glaux maritima</i>	—	—	9	1.2
<i>Plantago Coronopus</i>	4	0.4	1	0.1
<i>Triglochin maritimum</i>	—	—	1	0.1
<i>Aster Tripolium</i>	—	—	trace	—
Totals	1008	100.0	776	99.9
(b) Upper , with <i>Agrostis</i> , etc.,				
<i>Festuca rubra</i>	785	90.1	714	81.6
<i>Agrostis alba</i> var. <i>coarctata</i>	45	5.2	103	11.8
<i>Juncus Gerardi</i>	18	2.1	21	2.4
<i>Armeria maritima</i>	12	1.4	17	1.9
<i>Plantago Coronopus</i>	10	1.1	10	1.1
<i>Glaux maritima</i>	1	0.1	8	0.9
<i>Triglochin maritimum</i>	—	—	2	0.2
Totals	871	100.0	875	99.9

One further example may be given. An approximately circular piece of turf (3.5 inches = 9 cms. diameter), apparently containing a single large plant of *Armeria*, was taken from the **Armerietum** near Ynyslas. On analysis this yielded 240 unit shoots, made up as follows:

<i>Armeria maritima</i> ,	22 complete plants ¹ ,	with 182 unit shoots.
<i>Glyceria maritima</i> ,	24 tufted	„ ² „ 53 „ „
<i>Triglochin maritimum</i> ,	5 small	„ „ 5 „ „
Total	51 plants	with 240 „ „

¹ These included 1 main plant with 119 unit shoots; 1 plant with 17 units; 1 with 12; 1 with 9; 1 with 6; 2 with 2; and 15 with only 1 shoot each (3 were young seedlings).

² Probably some of these were formerly connected; this would yield somewhat fewer plants.

These turf analyses may be taken as typical of the associations concerned. Of course samples taken from special places or transitional zones might give very different results. Apart from the absence in the particular samples selected of some of the less abundant species, the analyses serve to show the composition of the herbage and the degree of dominance of the dominant species. They also indicate the completeness with which the ground is covered by plants¹. The compactness and density of the turf have an important bearing on problems to be discussed later. Attention may also be drawn to the fact that the **Lower Festucetum** near Ynyslas contains less *Armeria*, and a markedly greater percentage of plants characteristic of higher levels (e.g. *Festuca*, *Juncus Gerardi* and *Plantago Coronopus*), than the corresponding sub-association near Glandovey. This fact has been corroborated by repeated field observations, and is probably correlated with the sandy, well-drained nature of the strip along the river bank at Ynyslas, on which the sub-association is developed. This point will be referred to again.

Vertical Ranges of the Associations.

Occasionally two zones or associations are abruptly separated from each other by a shallow escarpment. Such an escarpment occurs more frequently at the margin of the **Juncetum** than between the different sward associations (but cf. Pl. XII, Phot. 4). For the most part, however, the surface of the marsh is gently undulating in character; distinctly hummocky in newly developed marsh, but tending to become more level with increasing age. On this undulating surface the associations merge gradually into one another. A considerable number of levels were taken in order to ascertain the respective vertical ranges of the different associations². The following are the minimum and maximum readings obtained, which give the vertical ranges. No bench mark was available, so an arbitrary datum line (taken as zero) was selected

TABLE III. *Vertical Ranges of the Associations.*

	Near Ynyslas		Near Glandovey	
2. Glycerietum	0.00 feet to	1.30 feet	0.00 feet to	0.42 feet
3. Armerietum	1.00	2.06	0.46	1.13
4. Festucetum				
(a) Lower	1.60	2.30	1.23	2.87
(b) Upper	2.30	2.60	4.13	4.41
5. Juncetum	2.40	4.30	2.74	4.33
Unhealthy Juncetum			2.21	2.76

¹ It may be noted that the turf analysis yielding the smallest total of unit shoots (i.e. the **Armerietum** near Glandovey) works out at about 103.5 millions of unit shoots per acre; while the Ynyslas **Glycerietum** yields no less than 249 millions. These figures are extraordinarily high as compared with those given by **Armstrong** (1) and **Stapledon** (20). The apparent discrepancy is partly explained by the difference of method employed (see footnote 3 p. 71), and partly, no doubt, by the fine nature of the grasses and the compactness of the salt marsh turf.

² The Ynyslas levels and turfs for analysis were taken at A, Fig. 1: the Glandovey levels at C, but the turfs a little nearer Glandovey Station. The levels at A were taken indiscriminately, but those at C along a definite line which intersected all the zones, and included some very young marsh.

at each of the two localities. The datum line in the two cases does not necessarily represent the same absolute level.

Thus the entire vertical range of the four chief associations combined is less than 4·5 feet (= 1·37 metres). The individual ranges of these associations frequently overlap. One special case of overlap (probably correlated with soil and drainage) is that of the **Armerietum** and **Lower Festucetum** near Ynyslas (see § 6). The Glandovey readings require some comment. The **Upper Festucetum** is at an unusually high level, even above the **Juncetum**. In this instance the association was not typical, for it contained a high percentage of land weeds, and was, in fact, passing into alluvial pasture. The "unhealthy **Juncetum**" was situated below a small escarpment, above which healthy *Juncus* was dominant. It represents plants fallen from a higher level on the retreat of the escarpment. These plants had succeeded in re-establishing themselves at the lower level, but may be gradually dying out.

The vertical distribution of salt marsh plants is affected in the most pronounced manner by the frequency and duration of submergence, and is therefore largely dependent on tide levels. The following information respecting tidal rises and ranges in the Dovey Estuary is given on Admiralty Chart No. 1484. We are informed by the Hydrographic Department of the Admiralty that the observations on which these calculations are based were made in the year 1890, and that no observations were made in other parts of the Estuary¹.

			Mean Spring Rise	Neap Rise	Neap Range
Aberdovey Pier	14 ft. 3 in.	9 ft. 11 in.	6 ft. 3 in.
Tannery Point	11 ,, 11 ,,		
Fron Goch Point	10 ,, 2 ,,		
Glandovey Railway Bridge			7 ,, 6 ,,		

Observations near Ynyslas show that the **Juncetum** is only submerged during exceptional conditions of wind and tide, while the average spring tide just covers the **Lower Festucetum**. Ordinary neap tides do not reach the sward associations at all.

§ 3. NOTES ON THE HALOPHYTES OF THE DOVEY ESTUARY.

As is seen in Fig. 2 the abundant species are only some 15 in number. A few others occur, such as *Suaeda maritima*, but are nowhere common; e.g. *Suaeda* is confined to a few spots, along the margins of channels or streams.

¹ Unfortunately we have so far been unable to make direct observations ourselves, and the above information applies only to points along the north shore of the Estuary, while for the most part the salt marshes fringe the south shore (Fig. 1). Captain Enoch Lewis of Aberdovey, however, informs us that the mean spring rise at Ynyslas (probably observed at the lower, or seaward, road bridge over the Leri), is about 10 feet, and the neap range about 4 feet. The points at which the vertical ranges of the plant associations were measured are situated as follows: A (Fig. 1) is opposite a point about half way between Aberdovey and Tannery Point; while C lies south-west from Fron Goch Point.

The complete absence of such plants as the various species of *Statice* (= *Limonium*), also *Atriplex* (*Obione*) *portulacoides*, must be remarked; especially as *Atriplex* and several species of *Statice* occur in other localities, even along the coast of Wales. To what extent long continued and close grazing may affect the relative frequency of those species which are present, or determine the absence of others, is at present unknown¹.

Two striking features which most of the species share in common are the characteristic form of the leaves (usually simple and narrowly linear, see Fig. 3), and their glabrous surface. Warming² has called attention to the prevalence of simple, spathulate or obovate leaves, amongst the tropical halophytes of the West Indies, and Priestley³ to the glabrous character of pelophilous plants. The following Dovey species, however, show some degree of hairiness: *Armeria maritima*, peduncles hairy, and occasionally the leaves also slightly hairy (more frequently hairy in other habitats); *Plantago maritima* and *P. Coronopus*, often hairy in central parts of rosettes.

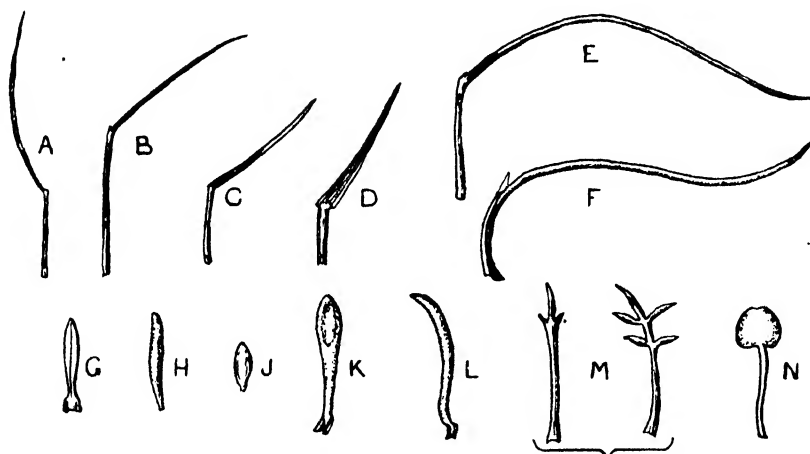


FIG. 3. Leaves of characteristic plants from closely grazed sward. Nine families are represented. A, *Festuca*. B, *Glyceria*. C, *Lepturus*. D, *Agrostis*. E, *Juncus Gerardi*. F, *Triglochin*. G, *Armeria*. H, *Spergularia*. J, *Glaux*. K, *Aster*. L, *Plantago maritima*. M, *P. Coronopus*. N, *Cochlearia*. $\frac{1}{2}$ nat. size.

A consideration of the varied habits of the plants is of interest in connexion with their rôle as marsh builders. There is much in common between salt marsh and sand dune plants. Both are active geological agents in that they have the power of stabilizing a mobile substratum, and that by their continued upward growth they render possible the vertical extension of their habitat. On the one hand the dune, built of wind borne sand, may grow rapidly; but on the other, the upward extension of the marsh, formed as it is chiefly of water borne sediment, is accomplished much more slowly.

¹ Cf. the case cited by Darwin in the *Origin of Species* (4, pp. 51-2).

² Warming (22, pp. 175-6, and Fig. 1).

³ Priestley (18, p. 14).

Two main types (with modifications) of habit, the erect and creeping, may be distinguished.

(a) *Creeping*. Most of the grasses are stoloniferous, with abundant fibrous roots, e.g. *Glyceria*, *Festuca* and *Agrostis*. *Lepturus* is more erect and tufted in habit. *Glyceria* may be taken as an example. When colonizing bare silt, long creeping shoots are formed, which spread rapidly. Later, as the sward becomes higher and denser, the mode of growth changes. The main shoots take up a more erect position and grow slowly, or even die away; while a succession of lateral shoots of limited growth appears, giving the plant

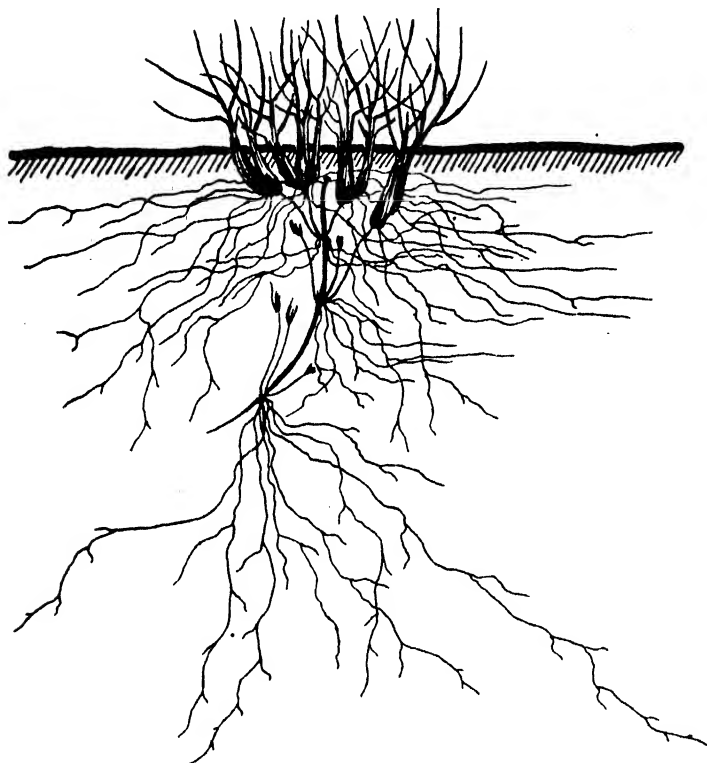


FIG. 4. Tufted form of *Glyceria maritima*. The "tillers" have been separated for convenience in drawing. $\frac{3}{4}$ nat. size.

a close, tufted habit (Fig. 4). In this condition considerable practice is required to distinguish *Glyceria* from the very similar tufted forms of *Festuca* and even *Lepturus*, especially as the grasses do not flower freely on the closely cropped sward. The dwarf, tufted growths of the three grasses can, however, be readily recognized, even in the vegetative condition, by colour characters¹.

¹ (1) *Glyceria*; leaves dull green, somewhat glaucous (fading to a pinkish colour). Lower leaf sheaths paler than in *Festuca*. Roots white.

(2) *Festuca*; leaves bright green (fading to yellow). Lower sheaths dark brown. Roots (except the youngest) brown.

Of other plants with creeping stems, the sympodial rhizomes of *Juncus* spp. are well known. *Triglochin* has stems which are either horizontal or more frequently ascending. When growing alone, it may give rise to tussocks of a characteristic form (Fig. 13). The creeping underground stems of *Glaux* produce numbers of winter buds (Fig. 5), and at the same time distribute them. The aerial shoots die down in autumn, and the strongly rooted buds rest during the winter, rapidly growing to the surface in spring.

(b) *Erect*. *Armeria* may be taken as a type. The plant has an elongated tap root, and a much branched shoot (Fig. 6). The number of branches increases with age, and their growth keeps pace with the slow accumulation of silt. The habit of *Plantago maritima* and of *P. Coronopus* is similar to that of *Armeria*, though *P. Coronopus*, with its shorter duration of life, is less often branched.

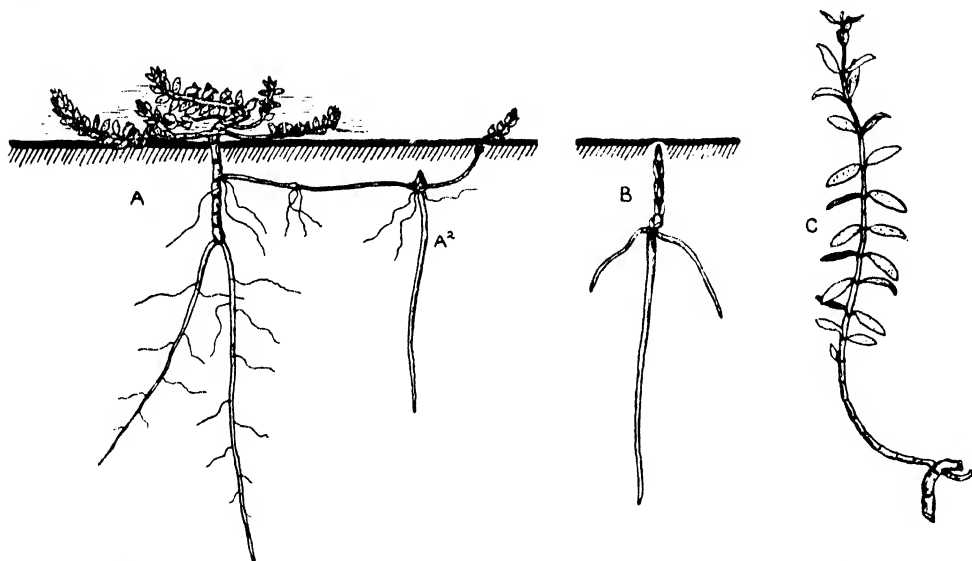


FIG. 5. *Glaux maritima*. A, sward plant in September, showing rooted winter bud (A^2). B, winter bud in February. C, part of aerial shoot of plant from *Juncetum* (September). All about $\frac{1}{2}$ nat. size.

Examples of rosette plants are furnished by *Armeria*, *Plantago* spp. and *Cochlearia*.

This heterogeneous assemblage of plants with their varied habits; their crowded shoots; their very numerous, often deeply penetrating roots, which interlock in every direction; their capacity of adjusting their positions in response to changes of level—is extremely effective for purposes of marsh building. The silt deposited by high tides on and between the shoots of the plants is incorporated and consolidated, and the level of the marsh slowly

(3) *Lepturus*; leaves scarcely so bright as *Festuca*, from which *Lepturus* can be distinguished by its more compact, stiffer, and more erect habit. *Roots yellow*.

The most reliable character is undoubtedly root colour, but to a trained eye, the more easily applied test of leaf colour is, in the case of grazed turf, sufficient in most cases.

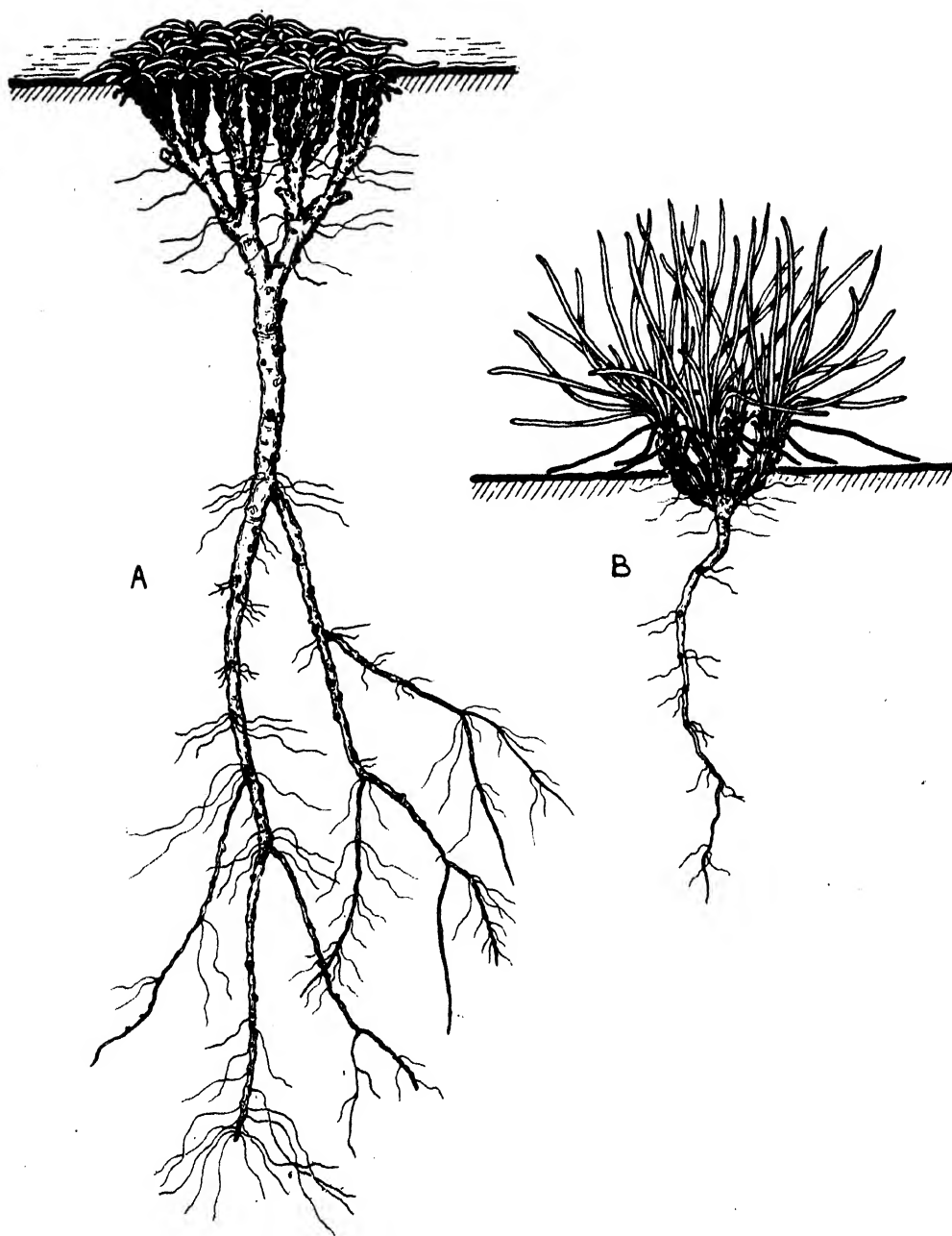


FIG. 6. *Armeria maritima* (= *Statice maritima*). A, from **Armerietum** sward.
B, from **Juncetum**. About $\frac{2}{3}$ nat. size.

raised. As this is accomplished the habitat conditions slowly change, and with them the vegetation. The various associations, which represent stages in the normal succession, have already been enumerated. The effectiveness of the plants as silt-binders is realized when one dissects turfs for analysis. Even a powerful, continuous stream of tap water directed on to the roots fails to remove the silt unless aided by constant manipulation. The extreme density of the covering of vegetation, together with its binding power, renders any breach of the surface of the sward by wave action difficult and unlikely. This power of resistance is aided by the fact that nearly all the sward plants (except *Glaux*) are evergreen perennials¹. Even *Lepturus*, stated by various authorities to be an annual, is perfectly fresh and green during the winter.

Finally, though no extended reference to the subject is possible here, it must be pointed out that a number of the characteristic, and even some of the dominant species, are not obligate salt marsh plants at all². Some species, for example, also occur, well above tide marks, as pioneers in the colonization of maritime rocks, e.g. *Armeria* and *Plantago maritima*. Under these circumstances the plants are pronounced chasmophytes. When more soil has collected in the clefts of the rocks, *Plantago Coronopus*, *Festuca rubra*, etc. may also be found. Several of the species, or very closely allied forms, are to be found on high mountains, e.g. *Armeria*, *Plantago maritima* and *Cochlearia*. Again, *Plantago maritima*, with or without *P. Coronopus*, is the chief constituent of the "Plantago sward" of the Faröes³ and the west coast of Ireland⁴.

§ 4. THE PRIMARY BUILDING OF THE SALT MARSH⁵.

At first sight a salt marsh, with its winding channels and innumerable "pans," presents many difficulties. The morphology of a mature marsh is complicated and intricate, and can only be interpreted in the light of ontogeny. For the most part the Dovey marshes are mature and apparently long established⁶. Only in a few spots, notably at C, Fig. 1, is primary marsh, i.e. that formed directly on bare silt, developing on any considerable scale at the present time. The development of such primary marsh may now be described.

In the Dovey Estuary, the **Salicornietum** is not, in most cases, developed in close proximity to the sward, and hence appears to play but a subordinate part in the building of permanent marsh (cf. **Oliver, 14**, and

¹ This statement applies particularly to the grazed sward of the Dovey marshes. The evergreen habit of certain species is not quite so pronounced in some other ungrazed marshes examined. Even then the underground parts persist.

² Cf. **Ostenfeld (16, p. 926)**.

³ **Ostenfeld (16, p. 929)**.

⁴ **Praeger (17, p. 10)**.

⁵ Cf. **Oliver (14)**, **Hill (8)**, and **Oliver (in 19, 2 II, pp. 141 et seq.)**.

⁶ No doubt considerable changes have taken place since the construction (during the years 1861-3) of this part of the Cambrian Railway; and the subsequent erection, to protect the railway embankments, of the numerous breakwaters (marked as projecting lines on the map forming Fig. 1).

19). So far as phanerogams are concerned¹, the earliest permanent colonizer is almost invariably *Glyceria*², which extends horizontally, collecting silt and forming low, flat hummocks. As the level is gradually raised, the *Glyceria* assumes the tufted form (see § 3), *Armeria* and other plants establish themselves, and frequently green algae³ appear between the shoots of the flowering plants. Thus is initiated the succession of associations described above (Fig. 7 and Pl. XIII, Phot. 5, 6 and 7). The primary hummocks continue to grow horizontally as well as vertically, for the peripheral fringe of *Glyceria*

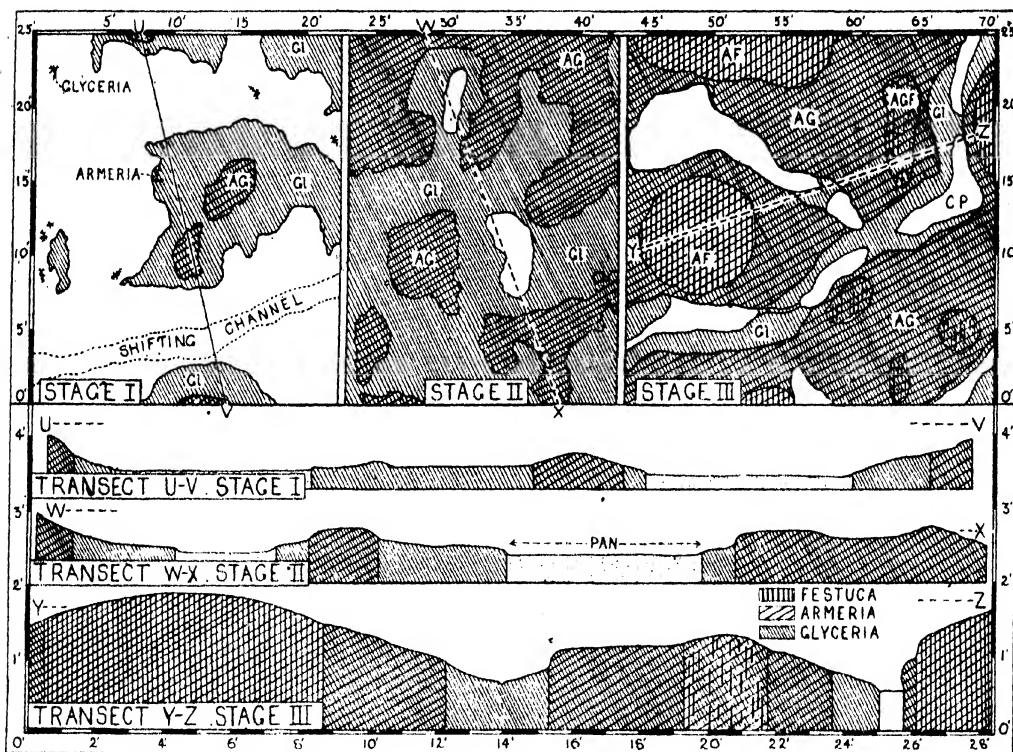


FIG. 7. Primary building of salt marsh. Three surveyed areas of marsh at C (Fig. 1) are shown, illustrating successive stages of development. GI, *Glycerietum*. AG, *Armerietum* with *Glyceria*. AF, *Lower Festucetum* with *Armeria*. In AGF, *Armeria* is associated with both *Glyceria* and *Festuca*. The respective hatchings used to denote presence of these dominant species are also employed in subsequent Figs. The three levelled transects have the same datum line, so that the relation of vegetation to altitude is clearly seen (vertical scale is twice the horizontal). Two primary depression pans are shown in Stage II (the larger is again seen in Pl. XIII, Phot. 6). CP (Stage III) is also seen in Pl. XV, Phot. 16.

¹ In this paper no account is taken of the part, doubtless an important one, played by algae in marsh building. The algae of the Dovey Estuary have not yet been worked out. Cf. Cotton (3, pp. 61 *et seq.*).

² Occasionally other species, such as *Spergularia media* or *Glaux*, may be found growing directly on otherwise bare silt. E.g. there are considerable patches of *Glaux* to the west of E, Fig. 1.

³ E.g. *Rhizoclonium riparium*, *Vaucheria* sp., *Enteromorpha* sp., *Lyngbya* sp. etc.; these were kindly examined by Mr Cotton.

still extends outwards on the silt. After a time the hummocks tend to coalesce, and the incipient sward to become more continuous (Fig. 7 II)¹. Until quite a late stage of development, however, the positions of the original primary hummocks are still recognizable as diminutive rounded peaks, occupied by what may be termed a "summit flora." The higher a hummock becomes, the fewer tides cover it, and the less silt is deposited. Hence, with increasing age, the hummocks grow more slowly in vertical extent. At the same time, the level of the lower, more frequently flooded intervening portions is raised comparatively rapidly. Thus the general surface of the marsh becomes more level and less hummocky. Owing to other causes, however, a uniform level is never attained. For instance, during high tides, as the channels become filled, the water tends to overflow their banks. When this happens, the coarser, heavier sediment is naturally deposited first, and so the banks of streams and the larger channels often become slightly raised above the surrounding level. This applies to the main river, as well as to tributary streams and channels (see Pl. XII, Phot. 1).

So far as the general distribution of plant associations is concerned, those characteristic of higher levels are usually found: (1) on the summits of the raised hummocks formed during early stages of marsh building; (2) in later stages, often fringing the banks of streams or large channels, especially in the more sandy areas, and (3) where a considerable width of marsh has been formed, on the relatively high ground remote from the river channel. No doubt this ground is often of greater age than that nearer the river, as e.g. much of the area occupied by *Juncetum* at E, Fig. 1. Here, on the inner side of the bend, the land slopes gradually upwards from the river.

At no stage is the vegetation which clothes the marsh entirely continuous. As the water retreats after high tides, it drains away between the hummocks of the developing marsh, and soon cuts shallow, winding channels in the silt. At first these primary drainage channels are shifting and ill-defined, but as development proceeds, the spreading vegetation tends to confine the channels within more definite limits (Pl. XIII, Phot. 5 and 7, and Fig. 7). Owing to the small angle of slope of the silt, the channels deepen little by erosion. Nevertheless, so long as there is sufficient scour to prevent accumulation of silt, on which plants might grow, they become deeper owing to the growth of the marsh in the vertical direction. As the whole marsh increases in surface extent the main channels lengthen, new tributaries arise, and finally drainage systems are established, comparable to those of a river basin on land.

In addition to the channels, which carry off the main flood water, and which from the first communicate directly with the estuary, subsidiary drainage hollows, the "pans," make their appearance². What may be called *primary pans*, or *primary depression pans*, arise in the following way. A group of

¹ Cf. *Hill* (8, Figs. 4 and 5).

² Cf. the drainage depressions in moorland peat, described in the Introduction, p. 38 (vol. 4).

hummocks may coalesce so as to enclose a shallow depression or hollow, which for a time remains filled with water when the high tides subside. Such hollows may possess partial outlets, in which case they usually become the sources of tributary channels. Frequently, however, outlets are completely wanting, and the depressions form incipient pans (Fig. 7 II, and Pl. XIII, Phot. 6). Whether outlets are present or not, depends on the topography of the system of hummocks, which determines how the surplus water shall drain away. Considerable scour is needed to prevent complete enclosure of the depression by a vigorous growth of *Glyceria*. If once the encircling process is completed, upward growth of the lower portions of the margin is comparatively rapid, and the pan becomes more and more isolated (cf. Pl. XII, Phot. 2). An incipient pan, then, always contains a residue of water after the final ebb of the spring tides. Drainage, of both salt and rain water, from the surrounding hummocks adds to this residual water, which can only escape slowly by percolation or evaporation. Thus the pans tend to remain filled for longer or shorter periods, and this inhibits the growth of vegetation. Temporary pans of this nature are sometimes found even in the **Salicornietum** (Pl. XIII, Phot. 8), but those which arise in the developing sward are numerous and remarkably persistent. Primary pans and channels thus originate contemporaneously with the sward itself, and represent parts on which vegetation cannot gain a foothold, owing to the effect of either stagnant or rushing water.

§ 5. SECONDARY CHANGES IN SURFACE RELIEF.

(a) *Marginal Erosion and Formation of Secondary Marsh.*

Considerable stress has been laid on the dense nature of the vegetation, and the efficiency of its component plants as silt-binders. When once formed, the sward is so compact that, in a more or less sheltered estuary, wave action has little or no effect in abrading its surface. Yet the marsh is not without its weak spots, where erosion, and consequently retrogression, may occur. One such spot is the river-side margin of the marsh.

So long as the primary hummocks are but slightly raised above the level of the silt, they present little opportunity for wave attack. But when the horizontal limit of extension of the marsh has been reached, while vertical growth still continues, its flanks become vulnerable, and tidal erosion takes place along the margin. A low, irregular escarpment is formed, which is gradually undermined by the scouring action of the tides (Pl. XIV, Phot. 9). Larger or smaller masses of turf frequently break away and fall, and the marsh slowly retreats from the river front. Usually, however, this marginal retrogression is arrested, sooner or later, by the formation of secondary marsh below the escarpment and at a lower level. For the most part, the blocks of turf remain where they fall, and form starting points for recolonization.

Glyceria rapidly extends from the detached turfs to the accumulating silt, and secondary sward is gradually formed¹ (Pl. XIV, Phot. 10, 11 and 12).

Secondary depression pans, and small secondary channels, are formed in the regenerated sward in much the same way as in primary marsh (Pl. XIV, Phot. 11). Secondary pans differ from primary in being more numerous, and also in that they, as well as the secondary channels, are usually deeper from the first, owing to the depth of the fallen hummocks amongst which they originate.

The secondary sward may in its turn be subjected to similar marginal erosion, and a second escarpment formed, more or less parallel to the first (Pl. XIV, Phot. 9). In some places no fewer than three such parallel escarpments are visible. Thus successive waves of retrogression followed by regeneration tend to spread over the marsh, profoundly modifying its original configuration². So far as our observations went, however, the cutting back of the scarps is not carried on indefinitely, but ceases after a time. As erosion diminishes, the escarpments gradually become more shallow, till finally the line of demarcation between primary and secondary sward tends to be obliterated.

Any alterations in direction or velocity of the tidal currents which directly affect the marsh (such as would be caused by changes in the main river channel, the construction of new breakwaters, etc.), might result in considerable local retrogression or extension. But considering the Dovey marshes as a whole, it would seem probable that at the present time retrogression and regeneration approximately keep pace with each other³.

(b) *Secondary Modifications of the Channels.*

Salt marsh channels are really small streams, which exhibit many of the phenomena associated with ordinary streams and rivers. They are peculiar, however, in several respects. For instance, their current is both reversible and intermittent: that is to say, the channels are tidal throughout their entire length, and their beds frequently dry up more or less completely between spring tides.

A noticeable feature of the larger channels of the Dovey marshes is their marked tendency to run, for the major part of their course, more or less

¹ *Armeria* is usually a prominent constituent of the flora of the fallen turfs. So far as our observations go, it seems probable that *Armeria* succeeds perfectly well in re-establishing itself at the lower level. Cf. Priestley (18, p. 17); also the case of *Juncus maritimus* mentioned above, p. 74.

² Priestley (18, pp. 13 and 15) speaks of denudation of the Severn marshes, but not of reconstruction.

³ No account is taken here of modifications which might be induced by secular movements, such as a general and gradual subsidence of the marsh, owing to packing and consolidation of the deep underlying deposits. No effects were observed which could be attributed to such a cause. Even granting a subsidence of this nature, it is possible that its effects would be so slow, in comparison with the normal changes proceeding on the surface of the marsh, as to be negligible.

parallel to the river¹. The course taken by these channels is possibly determined largely by the direction of flow of the tidal currents of the estuary itself. The raising, at an early stage, of the level of the river-side portion of the marsh, by the accumulation of more sediment than would reach parts further removed from the river (see above, p. 81; and Pl. XII, Phot. 1), would create a barrier behind which the channels would be confined. In the narrow area behind the barrier the channels would tend naturally to run parallel both to the barrier and the river, eventually turning to enter the latter. The case is probably analogous to that of streams which may run parallel to the shore line—often for miles—before entering the sea, owing to the accumulation of barriers of detritus by tidal currents and waves.

The courses of channels are frequently sinuous from the beginning, owing to the irregular arrangement of the hummocks amongst which they originate. Their winding character may be accentuated later, for erosion occurs on the outer or convex side of bends, and deposition of silt on the inner, concave side (Pl. XIII, Phot. 7). *Glyceria* spreads on this new silt, which is consolidated and its level gradually raised. Thus the channels may change their courses in the same way as do rivers on land².

During the flowing of a spring tide, the water rushes up the narrow channels with considerable noise and velocity, keeping them open and to some extent eroding their sides. There is here, on a smaller scale, the same incessant struggle between the forces of erosion and retrogression on the one hand, and those of deposition and consolidation on the other, as along the margin of the marsh. If for any reason the flow of water becomes insufficient to keep the channel completely open, one of two things may happen. Either (i) parts of the channel are roofed in, so that it becomes more or less subterranean; or (ii) it is converted into a chain of pans. The two processes are frequently met with in different parts of the same channel.

(i) *Formation of subterranean channels.* If the periodic rush of tidal waters is no longer sufficient to keep a fairly wide channel completely open³, silt may accumulate along the sides of its bed. *Glyceria* colonizes the silt and invades the channel (Pl. XV, Phot. 13). Gradually the sides are built up and the channel narrowed (Pl. XV, Phot. 14, and Fig. 8). Usually it remains comparatively deep, for the water, though reduced in volume, is still sufficient

¹ This tendency is less pronounced in the broadest parts of the marshes (e.g. at D, Fig. 1; Pl. XII, Phot. 1), but is invariably found where the total width of the marshland is not very great, e.g. at A and C, Fig. 1. Near A two separate measured lines gave 319 feet (= 97.2 metres) and 487 feet (= 148.4 metres) respectively as the total breadth of the marsh, including the *Juncetum*, which is well above the level of the channels. At C, a corresponding line gave 348 feet (= 106.1 metres).

² It seems not improbable that in some cases two or more meandering channels may ultimately combine for part of their courses, and that something analogous to "river capture" may occur. This and other points have not yet been fully worked out.

³ This may be due to any one of a number of causes, such as partial blocking of the channel by fallen turf; deflection of part of the current by "river capture," etc., see also p. 86.

to keep a narrow channel open. As the level of the new turf rises, *Armeria*, *Spergularia* and other plants follow *Glyceria* in normal succession. When a stage is reached such as that shown in Phot. 14 (Pl. XV) and Fig. 8 III, stolons of *Glyceria* frequently cross the narrow channel and become entangled with similar shoots from the opposite bank. Silt is rapidly collected by the

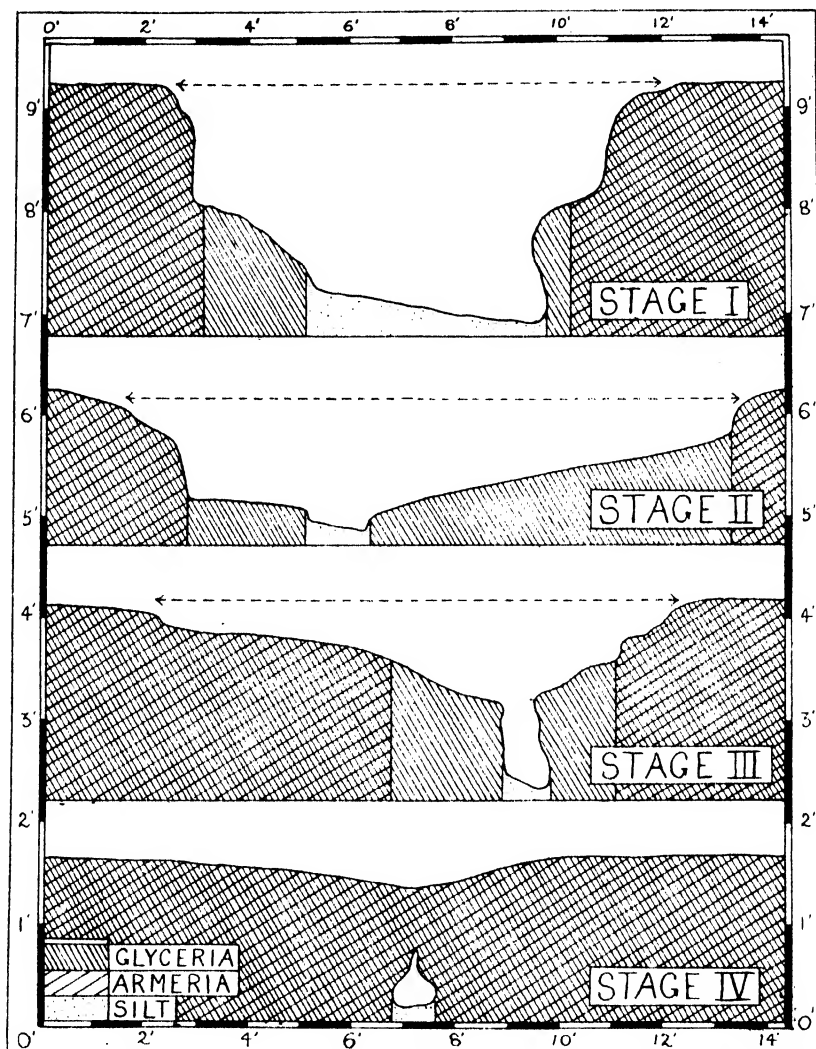


FIG. 8. Levelled transects of four channels (near A, Fig. 1), to illustrate stages in formation of subterranean channels. Hatching refers to dominant species occupying the surface, while the barbed, dotted lines give the original widths of the respective channels. The vertical scale is twice the horizontal.

intertwined shoots, and firm little bridges formed across the channel. The roofing-in process may be continued till the position of the channel is only indicated by a line of longer or shorter apertures (Pl. XV, Phot. 15). By this time the raising of the level of the new turf may have rendered the original

banks of the channel indistinct, though as a rule they are clearly visible till a late stage (Pl. XV, Phot. 14 and Fig. 8). Finally, the original banks may be entirely obliterated, and the channel, at least for certain parts of its course, completely roofed in. Nothing now remains to mark its position except an occasional aperture.

There can be no doubt that the subterranean channels of the Dovey marshes are formed, at least in the great majority of cases, in the manner just described. No evidence was forthcoming to show that they ever originate either below the surface or from sun cracks¹.

(ii) *Formation of "channel pans."* Only shallow channels, or those with shallow parts extending right across the bed, can give rise to channel pans. These are usually either comparatively young channels, or older ones which have been partially silted up. It should be noted that channels which become subterranean are always relatively deep. Channel pans very often occur in the upper reaches of a channel, especially a tributary one. A number of cases were seen in which the upper part of a channel had been converted into a chain of pans, while the lower portion had become more or less subterranean. In Pl. XIII, Phot. 7, an accumulation of silt is seen to have formed across a fairly young channel. Should circumstances be favourable, *Glyceria* will extend on to the silt, and as usual proceed to collect more sediment. If once *Glyceria* succeeds in establishing itself across the channel, the latter will probably be permanently blocked at this point (Pl. XV, Phot. 16, and Fig. 7 III). Similar obstructions may arise elsewhere in the course of the channel, which thus becomes, at least in part, cut up into a series of elongated, incipient pans. Phot. 17 (Pl. XVI) shows a chain of channel pans arising from an older channel, the entire bed of which had been to a great extent silted up. When once the process has commenced, vegetation tends to invade the now stagnant channel at many points. But, as in the formation of primary marsh, the invading vegetation can never become established in the deeper parts, which remain as drainage hollows, and so give rise to channel pans. The surrounding sward may be built up to the general marsh level, and only the position of the pans, in a linear series, be left to indicate their mode of origin (Pl. XVI, Phot. 18). After their formation, channel pans are subject to further modification, as described below.

(c) *Pans and their Fate.*

i. *Origin.* Three different methods of pan formation have been described above. (1) *Primary pans*, or *primary depression pans*, originate on developing primary marsh, and are contemporaneous with the sward that bounds them.

¹ Sun cracks are regularly seen in open pans, etc. (Pl. XIII, Phot. 8), and may occasionally be formed in the sward itself during droughts, but even then only with difficulty, owing to the binding power of the matted roots. Sun cracks do not appear to play any very important part in modifying the surface features of the marshes.

Secondary pans originate subsequently, and may be either (2) *Secondary depression pans*, which arise like primary pans, but on secondary marsh; or (3) *Channel pans*, formed by the blocking of a shallow channel at various points. Owing to the manifold changes which the surface relief of a mature marsh has undergone, it is difficult to estimate the relative numbers of pans which owe their origin to these three methods respectively. The majority of those on secondary marsh are probably secondary depression pans; while on old primary marsh a large number have no doubt originated as channel pans. The only other mode of origin actually observed on the Dovey marshes is the secondary formation of smaller pans during the recolonization of larger (usually compound) ones. When a large pan is recolonized by vegetation, it frequently happens that one, or it may be several, permanent subsidiary drainage hollows are left, which the plants cannot successfully invade. These appear to form the starting points of what are virtually new pans, which, from their mode of origin, may be termed (4) *Residual pans* (Pl. XV, Phot. 15, and Fig. 12). This fourth class, however, is scarcely so distinct as the other three.

It should be noted that in all four methods enumerated above, the pans originate on bare silt, and not on the plant-covered surface of the marsh. No evidence whatever was forthcoming to suggest that pans ever arise *de novo* on existing turf, in consequence of injury to or destruction of its surface. Careful search for such evidence was made, in view of the opinion expressed by Warming, that pans are often formed where the turf has been weakened or destroyed by putrefying masses of algae or *Zostera*, or by the treading of cattle. These weak spots are, he thinks, subsequently excavated by the sea¹. An experiment was made near Ynyslas, to see how far the waves would excavate further an artificially prepared weak spot. On August 20th, 1914, a nearly circular piece of *Armerietum* turf (about 18 inches diameter) was completely removed, including the roots; an artificial pan, 4 inches in depth, being left. Nearly 17 months later (January 8th, 1916) this pan was again examined. So far from being further excavated, its depth was now only 3 inches, while its diameter was slightly less than at first, owing to overgrowth of the margins (cf. p. 94). On October 3rd, 1916, the pan was a little deeper (3.5-4 inches), but its diameter was unchanged. One *Salicornia* and four plants of *Glyceria* had invaded the pan. Too much stress should not be laid on the absence of erosion during the two years of this single experiment. Other evidence, however, such as the compact, resistant nature of the sward, and the slow rate at which erosion of active pans appears to proceed (see p. 90), renders it difficult to believe that pans can often arise directly on the turf in the way suggested by Warming. Of course in some estuaries wave action may be more potent than in the Dovey.

¹ Warming (23, pp. 43-47, also *résumé* in French, p. 56). This is the only important account of salt marsh pans we have seen; it contains many interesting observations. Warming is of opinion (p. 45) that pans may originate in a variety of ways.

No doubt there are methods by which pans can be formed, other than those described by Warming and in this paper¹. Indeed, it is probably not going too far to say that *pans may originate from any hollow or depression, no matter how formed, in which water collects during spring tides, and remains sufficiently long to prevent successful invasion by marsh vegetation.*

ii. *Modifications due to Erosion, etc.* Whatever their mode of origin, pans may subsequently undergo changes of many kinds; they may either increase or diminish in size, alter their shapes, change their positions, or even disappear altogether.

The mechanical effect of the tides is less in the case of pans than along the riverside margin of the marsh; yet here too, as the sides of a pan are raised by deposition, they become more liable to erosion. The rate at which pans

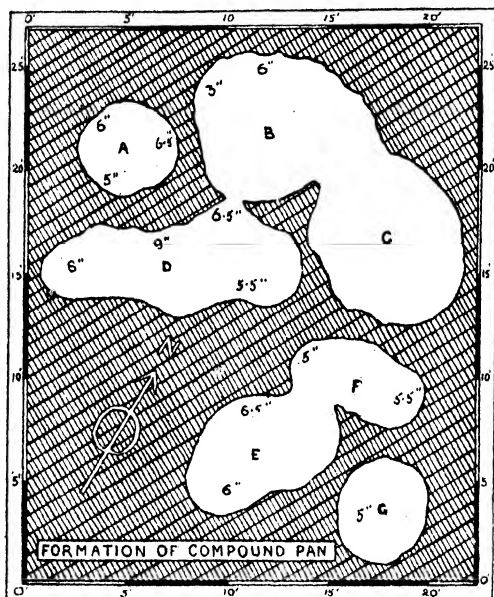


FIG. 9. System of active pans on *Armeria* (sandy marsh, A, Fig. 1), described in text. Figures refer to depths of pans. A photograph of this system is seen on Pl. XVI, Phot. 19.

enlarge by the undercutting of their sides varies in different cases. Probably it is always relatively slow, but most rapid where the soil is sandy, both on account of the more easily weathered substratum, and because the sand grains increase the erosive power of the water. The outlines of pans are very diverse; some are elongated, others curved, a few are branched, while a considerable number are roughly circular in shape. In general, there is a marked tendency to assume a rounded rather than an angular form. How far this tendency can actually be realized depends on various factors. No doubt the original shape of the pan is important; also the direction from which

¹ Professor F. W. Oliver has, in fact, observed several other methods on the marshes of the Bouche d'Erquy.

the water enters the pan for the first time during spring tides. As the water enters a pan, an eddy is frequently produced, and the water tends to sweep round the pan with a circular movement, eroding projecting or angular portions of the sides more than less prominent parts. As time goes on, the pan thus becomes more and more circular in outline (Figs. 9 and 10, and

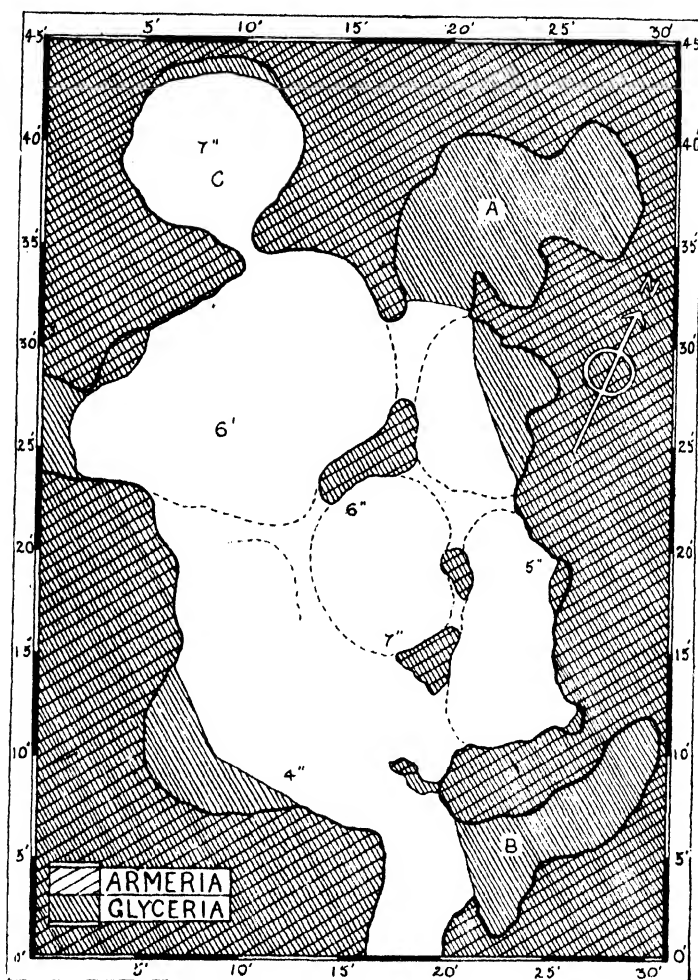


FIG 10. Large compound pan on *Armeria* (at A, Fig. 1). A and B are pans at a somewhat higher level, which have been drained by connection with the main pan, and are completely carpeted by *Glyceria*. C has become connected more recently. *Glyceria* has also invaded the main pan at certain points. The "islands" faintly suggest former positions of some of the smaller units which contributed to formation of the compound pan (cf. Pl. XVI, Phot. 20). Dotted lines indicate the kind of way in which the "islands" may have been formerly connected with mainland. Figures give depths in inches.

Pl. XVI, Phot. 19). The action is almost exactly analogous to that by which "pot holes" are produced in a rocky river bed. As is to be expected, circular pans are met with much more frequently on sandy than on muddy areas.

When several neighbouring pans are enlarging simultaneously, they may coalesce and combine to form one large *compound pan*. All stages in the formation of such compound pans are frequently met with, especially on low-lying, sandy marsh, such as the **Armerietum** near Ynyslas (Figs. 9, 10 and 12, and Pl. XVI, Phot. 19 and 20). The size of the smallest simple pans may not exceed 1 to 3 feet in diameter, but compound pans often attain a considerable size. The largest one seen was 57 feet 6 inches (= 17.25 metres) long, by 20 feet 9 inches (= 6.25 metres) wide. Occasionally channel pans are even longer than this, though much narrower. Fig. 9 and Phot. 19 (Pl. XVI) illustrate a system of pans in all of which active erosion is in progress. Pans B, C and D are already connected, and so are E and F. There is little doubt that ultimately all the pans (A-G) will coalesce and form one large compound pan. With regard to the rate of erosion of these pans, the following measurements afford the only data yet available:

	August 20, 1914	January 8, 1916	October 3, 1916
Narrowest part of neck separating A and B	12.0 inches	10.0 inches	9.0 inches
" " " " C " D	5.0 "	4.5 "	3.5 "
" " " " C " F	12.5 "	12.0 "	12.0 "
" " " " E " G	12.0 "	—	11.0 "
Width of opening between B " D	8.0 "	13.0 "	14.0 "

Not infrequently a pan may be extending in one direction owing to erosion, while at the same time another part is being silted up and invaded by vegetation. Thus, just as channels may change their courses, so pans may slowly alter their positions. Unless, however, they become secondarily connected with channels or other pans, such meandering pans retain their individuality.

The history of individual pans is often obscure, and difficult to unravel. Fig. 11 represents an attempt to trace the history of two pans, the positions of which suggested a possible origin as channel pans, formerly connected with the channel shown in the same figure¹.

Ordinary pans are entirely bare of phanerogamic vegetation, and the mobile silt forming their floors is therefore devoid of roots, at least in the position of growth. If, however, the sides of a pan are retreating, one finds such roots near the eroded sides, and these afford definite evidence of the erosion. The method adopted, then, was to dig trenches across the pans, and carefully map the exposed sections, showing in particular the distribution of silt with and without roots respectively. Two such sections were cut (A-B and C-D). In both pans the abrupt fall, at certain points, of the line separating rootless silt from that with roots, suggested the former existence of a channel, the sectional outline of which was similar (except in size) in the

¹ Unfortunately, time did not permit of the completion even of this one experiment. The method may prove a useful one, though somewhat tedious, and difficult to employ except with a fairly sandy substratum. The results, though incomplete, appear of sufficient interest to put on record.

two cases. On the supposition that such a channel existed, and was subsequently converted into channel pans; the increase in size of the pans, as the marsh was gradually built up, is clearly indicated in the sections. One point of difficulty is the presence of old, much decayed roots underlying the supposed channel. A possible explanation of this is that the channel, as it shifted its course, came to traverse ground formerly occupied by sward. It

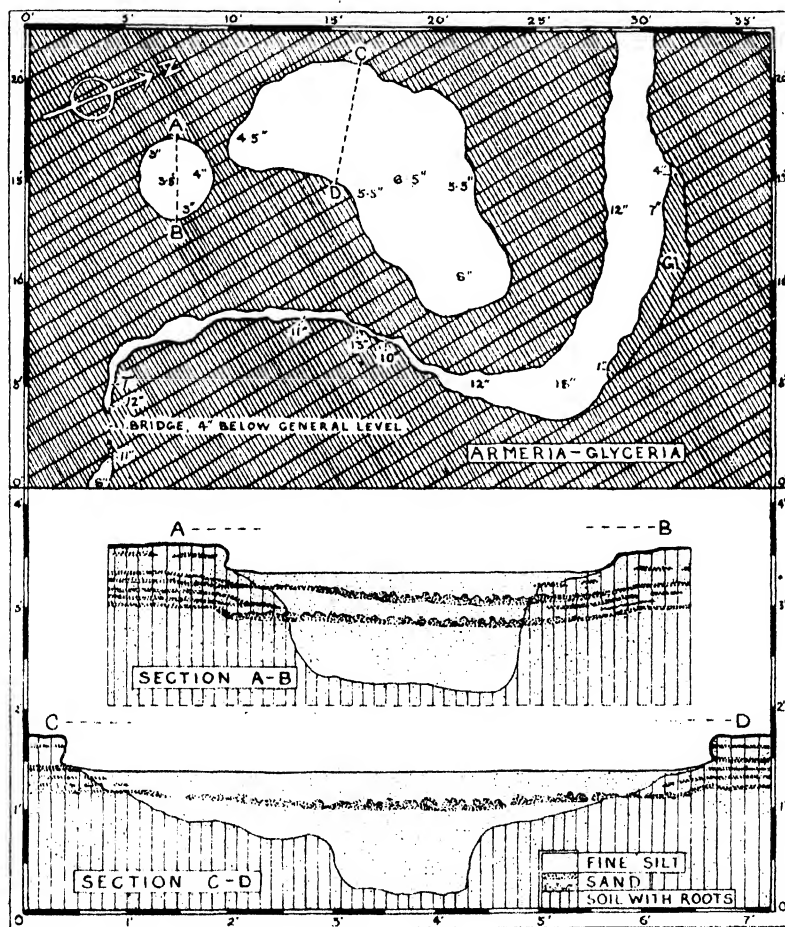


FIG. 11. A channel and two pans (which possibly originated as channel pans, see text). *Armerietum*, A, Fig. 1. Figures give depths in inches. In the sections, the vertical scale is the same as the horizontal.

is of course also possible, though perhaps less likely, that the pans originated directly on sward, in the way suggested by Warming. Another feature of interest is the alternating layers of silt and sand, the latter merging into one or two broad, irregular bands underlying the pans. These layers of sand increase in number and thickness towards the still more sandy strip of marsh bordering on the river. No doubt the sandy strata represent wind storms,

during which quantities of sand were blown over the marsh, most being intercepted along the river edge¹.

iii. *Persistence of pans.* The one condition necessary for the maintenance of a pan, not less than for its original formation, is the presence of a pool of salt water. This may dry up at intervals, but the periods of submergence are usually sufficiently long to prevent successful invasion by salt marsh plants. When once a pan is formed, it tends to persist. As the level of the marsh rises, the floors of the pans rise too, though more slowly, for silt deposited in the pans remains mobile and removable, while that deposited on the sward is consolidated by the vegetation. Thus, up to a certain point, the depth of pans gradually increases with age². On sandy areas the pans are usually fairly shallow, especially the large compound ones. Near Ynyslas a considerable number were measured, the depths varying from 2 inches to 2 feet 7 inches (say 5–80 cms.). The average was about 8 inches (20 cms.) or less. On the more muddy marsh towards the head of the estuary the average depth is greater, 12–18 inches (30–46 cms.) or even more being common (compare Photos. 2, 18, 21 with 19, 20 and 22).

Were there no process to compensate that of erosion, the surface of the marsh would sooner or later be more or less denuded of vegetation. Under certain conditions, however, pans become quiescent and gradually overgrown by vegetation. This may take place both in “high level” (e.g. **Upper Festucetum**, etc.) and “low level” (e.g. **Armerietum**) pans. Invasion of high level pans is no doubt assisted by the fact that they are filled by fewer tides, the intervening dry periods being therefore longer. The process at best is only a slow one, for less silt is available for levelling up the pans, and so they still act to some extent as drainage hollows. Sandy soil hastens the process, owing to more rapid percolation. Thus as a rule, the higher zones possess fewer pans than the lower³. Many pans are found, however, even in lower zones such as the **Armerietum**, which are more or less completely carpeted by vegetation (Pl. XV and XVI, Phot. 15 and 22, also Figs. 10 and 12). An examination of large numbers of these showed that in all cases drainage outlets had been established. Natural drainage is usually the indirect result of erosion⁴. We have seen that as a pan extends, it often becomes connected

¹ Compare the respective amounts of sand in the mechanical analyses on p. 67.

² No definite cases of disappearance of pans through silting up were observed, at all events in the lower zones of vegetation. In fact, in most cases silt is probably washed out of a pan practically as fast as it is deposited, until the pan reaches a certain depth. The depth attained may well be regulated by the relative ease or difficulty with which silt is removed by tides.

³ Pans in the **Juncetum** are few, but apparently very persistent, and are often more or less permanently filled with water. Here percolation is slow, and also evaporation, owing to protection by the taller vegetation.

⁴ Possibly a part—even an important part—may be played by burrowing animals such as crabs, both in forming drainage outlets and in the general erosion of pans. This has not yet been investigated. It may, however, be remarked that crabs appear to be less abundant here than in many marshes. Even their dead remains are infrequent.

Two other constructive processes, of minor importance, must be briefly described. These are (a) marginal overgrowth, and (b) tussock formation.

(a) *Marginal overgrowth*. In some cases a pan appears to be actively enlarging, when in reality the converse process is going on, and its area is slowly diminishing. This is especially noticeable in the deep pans towards the head of the estuary. Plants fringing the margins of a deep pan, including even those such as *Armeria*, with an erect habit of growth, slowly extend in the lateral or horizontal, as well as the vertical direction. Silt is trapped, and gradually a firm, overhanging margin is produced, in a somewhat similar manner as the land bridges over narrowing channels (p. 85). In this way the periphery of the pan slowly contracts, though at first sight the overhanging sides suggest that they are being undermined (cf. Pl. XVI, Phot. 21). Overhang may, in fact, be produced either by erosion with undercutting, or by marginal overgrowth. Care is needed to distinguish between these two cases. Where erosion is active, individual plants are often found dissected out from the turf, still attached, it may be, by their roots (*Armeria* is a particularly useful

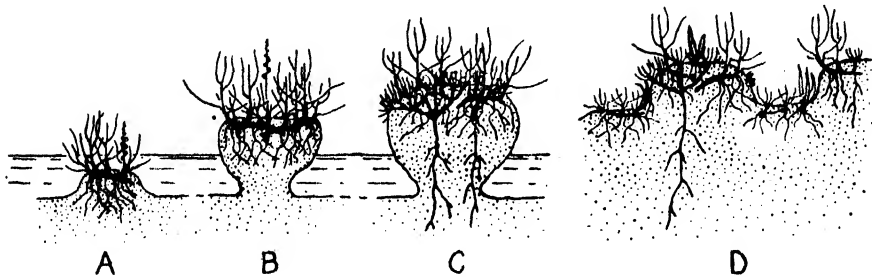


FIG. 13. Diagrammatic sections showing stages (A-D) in the formation of *Triglochin* tussocks, and their subsequent coalescence to form tussocky sward. In A and B, *Triglochin* alone is present. *Armeria* is added in C, and grasses and *Aster* in D.

index plant). Other roots, still in the position of growth, usually occur at or just below the surface of the pan bottom (see Fig. 11). In the case of overgrowth, on the other hand, such signs of erosion are absent, and the margin is compact, smooth and often rounded, in contrast to the more or less ragged, angular edge of an enlarging pan (cf. Pl. XVI, Phot. 18, 19, 21, etc.). In some instances undermining (due to scour or burrowing animals) may be in progress at or near the floor level, while overgrowth is simultaneously taking place above. This of course increases the overhang of the sides.

(b) *Tussock formation*. Occasionally colonization, whether of pans, old disused channels, or low, swampy ground, may proceed by a somewhat different method from those described above. Steep-sided, isolated tussocks are formed, in the building of which *Triglochin maritimum* (rather than *Glyceria*) plays the most important part¹. One or more plants of *Triglochin*

¹ The only spot in the whole of the Dovey Estuary where this was observed is a small area of marsh on the outer side of the river bend, between Glandovey and Dovey Junction (near F, Fig. 1). Here, patches of ill-drained ground, also some large, lagoon-like pans, have been

establish themselves on a spot of unoccupied silt, their sympodial rhizomes growing outwards and upwards. As the branches become more crowded, the upward growth is accentuated. Silt is collected as usual, and tussocks, shaped like a solid basin, are produced (Fig. 13 A and B)¹. At first the tussocks are firmly attached by roots to the substratum, but later they become unstable—sometimes even completely free—owing to the death and decay of the older rhizomes and roots at the base. The unattached tussocks may again become anchored by the long tap roots of *Armeria*, which often establishes itself on the summit of a tussock (Fig. 13 C). Other halophytes appear, and finally, if the exigencies of drainage permit, marginal overgrowth, together with the accumulation of silt between the tussocks, and its covering by vegetation, may result in the building of a more or less continuous turf. The irregular, tussocky appearance of sward formed in this manner is quite different from the undulating, rolling surface produced where *Glyceria* fills the rôle of pioneer.

iv. *Pan floras*. (a) The flora of *undrained pans*, whether quiescent or actively enlarging, is meagre. The algae have not yet been studied, but a number of species (usually small ones) occur, and may play an important part in stabilizing the mobile substratum². Of flowering plants, *Ruppia maritima*, in very wet pans; *Scirpus maritimus*, in a few old pans near Glandovey, and *Triglochin maritimum*, which sometimes follows *Scirpus* if the water is sufficiently shallow (Fig. 13), were the only species recorded³.

(b) *Drained pans*, on the other hand, become gradually colonized by the ordinary marsh halophytes. *Low level pans* (especially in the **Armerietum**), when provided with drainage outlets, are practically always invaded first by *Glyceria*, often accompanied by a few dwarf Salicornias. *Spergularia media* and *Armeria* usually follow, and the carpet of vegetation passes through the invaded in this manner. In some other marshes colonization by similar steep-sided tussocks seems to be a more important phenomenon, e.g. Dundrum Inner Harbour, and the head of Larne Lough, both on the east coast of Ireland.

¹ This is analogous to the marginal overgrowth of pans, but here growth is centrifugal, whereas in pans it is centripetal. **Warming** (23, p. 46, and Figs. 8 and 9) describes hummocks of *Triglochin*, each standing in the centre of a pan, surrounded by water. "like an old castle in its moat." He evidently regards the "moat" as having been excavated by waves, and the central hummock as a portion which had resisted erosion. The tussocks described above are undoubtedly due to a constructive rather than a destructive process, though at first sight they somewhat resemble the "islands" left during the formation of compound pans (see Pl. XVI, Phot. 20).

² A systematic examination of the algal flora of pans of various kinds would no doubt yield valuable results. Permanently wet pans should be contrasted both with completely drained pans and with those which retain their water for longer or shorter periods. Again, the levels at which the pans occur, and the character and degree of mobility of the substratum, are probably important. **Warming** (23, pp. 43-44) mentions a number of algae found in pans. He remarks that they are often advanced in decay, and do not thrive in the stagnant water, which is often much heated in summer.

³ **Warming** (23, p. 44) mentions also *Zannichellia* and *Potamogeton pectinatus*, and states that on the east coast of Denmark (where of course the water is less salt) the pans are sometimes filled with *Batrachium Baudotii*.

normal succession. For a long time the reclaimed pan is easily recognized by its somewhat depressed surface, and by the fact that its vegetation represents a lower stage in the succession than that of the surrounding sward (Pl. XV and XVI, Phot. 15 and 22, and Figs. 10 and 12). Ultimately the floor of the pan may reach the general level, when it entirely disappears.

High level pans (especially in the **Festucetum**) rarely have definite drainage outlets. Colonization appears to be a slow and difficult process, for the pans can only be said to be drained in the sense that the soil is often more or less sandy, while submergences are relatively infrequent. The pioneer plants differ from those found in low level pans. Small tufts of *Glyceria* occasionally occur, but play a subordinate part. *Glauz* and *Triglochin* are the two most frequent invaders, though *Spergularia*, *Agrostis* and other species are also found.

§ 6. PHYSIOLOGICAL NOTES.

As stated in the Introduction, the work embodied in this paper is of a preliminary character. The ultimate problems of plant distribution are to a great extent physiological problems of an extremely complex nature. They require the investigation not only of a number of physical and chemical factors, but also of the subtle relations between the plants themselves which we include under the term competition. Any detailed discussion of the factors which determine the distribution of the plants dealt with is beyond the scope of this paper, for most of them have still to be investigated. A few general remarks only will be offered.

In the case of plants living between tide marks, all the evidence points to the extreme importance of the frequency and duration of the periods of submergence and emergence respectively¹. From observations recorded above, it would seem probable that a sandy, porous soil, where percolation, and therefore drainage, is relatively rapid, to some extent compensates for more frequent and longer periods of submergence. Thus on the sandy marsh at Ynyslas, not only does the **Lower Festucetum** range lower² than at Glandovey (p. 74), but it also contains a greater proportion of plants characteristic of the **Upper Festucetum** (p. 72). This suggests the probable importance of root aeration, a suggestion which appears, at first sight, to be borne out by water-content analyses; the sandy soil invariably containing a much smaller percentage of water. But the problem is more complex than this, for chemical analyses show that the percentages of salt and organic matter are also much lower in sandy than muddy soils³. A series of careful

¹ This is well brought out by **Johnson** and **York** (9); see pp. 131-143 for a discussion of the effects of tidal changes on various factors affecting plant life. **Baker** and **Bohling** (2) emphasize the same point for the Brown Algae of the salt marsh.

² Relatively to the **Armerietum**.

³ The averages of a number of analyses taken near Ynyslas, from December to May, are as follows:

(a) *Water-content*. Upper 12 inches of sandy soil, with **Festucetum**, 24.3 % of water.

autecological studies, carried out on some half dozen characteristic species, with adequate experimental work, would no doubt throw much light on the subject, and help to disentangle the effects of the various factors.

With regard to the paucity of the flora of undrained pans, there can be little doubt that prolonged submergence after high tides effectually prevents in most cases the ordinary salt marsh plants from successfully invading the pans. The period during which water remains in undrained pans varies in different cases. Even in fairly sandy marsh it is usual for the pans to contain water for at least 8–14 days per month, while in some cases the pans are never completely dry. Thus pans are usually submerged for far longer periods than even the lowest of the sward zones. Granted then, on the one hand, that prolonged submergence prevents the growth of ordinary marsh halophytes, it may well be, on the other, that the periodic drying prevents successful invasion by aquatic flowering plants. In brief, the pans are probably too wet for most marsh halophytes, and too dry for true aquatics. But here again, the decisive factors (e.g. aeration, salinity¹, etc.) require to be elucidated by experiment.

§ 7. ECONOMIC IMPORTANCE OF THE MARSHES.

The Dovey marshes are of considerable agricultural importance as pasture lands for sheep. They have been grazed continuously for many years, at least as far back as the memory of the oldest farmers in the district. The sheep prefer the salt marsh sward to ordinary pastures, and thrive and fatten on it quickly. Practically all the species found on permanent marsh are eaten, except *Juncus maritimus*, which possesses, so far as we know, no economic value. So closely are the various sward zones grazed, that the herbage is rarely more than 1–2 inches (= 2·5–5 cms.) high. The belief is prevalent amongst farmers that the leaves of *Armeria*—for which the sheep show a distinct preference—are more nourishing than those of other plants. *Glyceria* is considered to have a low feeding value, while the **Upper Festucetum** is somewhat similar to certain mountain pastures. The most important sward zones then, from the point of view of sheep pasturage, are the **Armerietum** and **Lower Festucetum** (with *Armeria*)².

Finer soil, with **Armerietum** (including the comparatively dry and sandy second 4 inches—see mechanical analyses, p. 67), 38·6 %. Ratio 1·0 : 1·6.

(b) *Salt-content*, calculated as percentage of chlorine to dry weight of soil; **Festucetum**, 32 %, **Armerietum**, 58 %. Ratio 1·0 : 1·8.

(c) *Organic matter*, also calculated on dry weight of soil. **Festucetum**, 4·3 %, **Armerietum**, 9·5 %. Ratio 1·0 : 2·2.

¹ The salinity of the surface layers of soil in a dry pan is sometimes very high. The highest yet recorded (April 1914) was 2·16 % (estimated as chlorine, see previous footnote) for the top one inch of soil of a pan floor. Cf. the efflorescence of salt seen in the compound pan in Pl. XVI, Phot. 20.

² Owing no doubt to less frequent submergence and, on the whole, better drainage (with consequently warmer soil), the growth of the herbage in spring is earlier, as is also florescence, in the **Lower Festucetum** than in the **Armerietum**. *Armeria*, for instance, is often in full flower some three weeks earlier on the former than on the latter.

Another reason for the value attached to the salt marshes as grazing lands is their freedom from the liver fluke parasite. *Limnaea truncatula*, the intermediate host of *Fasciola hepatica* (the liver fluke), is extremely common on the damp, marshy pastures of the Dovey Flats, where the fluke disease has caused heavy losses to farmers. It is, however, entirely absent from lands under the influence of salt or brackish water. In some cases the snail (*Limnaea*) may be found within a few yards of the landward limit of the halophytic flora¹. To lowland farmers then, the possession of an area of salt marsh is of great importance: (1) on account of the high feeding value of the herbage, and (2) because the use of the more marshy ordinary pastures during the rainy periods of late summer and autumn can to a certain extent be avoided. It is at such times that *Limnaea* attains its maximum distribution.

Seeing that the salt marshes of the British Isles, on which sheep and cattle are pastured, cover a very large total area, it is obvious that their improvement and extension are matters of direct economic importance. The following appear to be some of the more important problems in this connexion: (a) extension of the pasture areas by land reclamation (cf. evidence in 19); (b) increase of the sward surface by partially or wholly obliterating the unproductive pans², and (c) prevention, by diking or otherwise, of the spread of the economically useless **Juncetum**. At present this covers large areas of marsh (see Fig. 1).

A minor use to which the grazed sward of a salt marsh can be put is that of providing turf for golf- or bowling-greens. If the turf is carefully selected, it is excellent in quality. The best for this purpose is the **Upper Festucetum** sward. *Festuca rubra* yields an exceedingly fine, close turf, while the coarser mats of *Agrostis* are also good, provided they are kept closely mown. Turf containing many tap-rooted rosette plants, such as *Armeria* or *Plantago Coronopus*, should be rejected.

SUMMARY.

1. Zonation is very pronounced on the Dovey salt marshes, and the following five plant associations, corresponding to different altitudinal zones, can usually be distinguished: (1) **Salicornietum europaeae** (the lowest), (2) **Glycerietum maritimae**, (3) **Armerietum maritimae**, (4) **Festucetum rubrae** (Lower and Upper), and (5) **Juncetum maritimi** (the highest).

¹ The exact distribution of *L. truncatula* on the Dovey Flats has been worked out by Mr C. L. Walton, who finds that it is broadly coincident with that of clay (or silt).

² Drainage experiments are occasionally tried by individual farmers. Usually these are of a desultory nature, but in a few cases more methodical drainage has been attempted, e.g. of the sward area at G, Fig. 1. Here the pans have been, to a considerable extent, got rid of. An exact survey of an area of marsh comprising about 4264 square yards (at A, Fig. 1) showed that a little more than 10 % of the surface was occupied by bare pans. In many parts the percentage is distinctly higher than this, at least for the lower zones (cf. Pl. XII, Phot. 2).

Associations (2), (3) and (4) give rise to a dwarf sward, valuable as sheep pasturage, while the **Juncetum** (5) forms a different and taller type of vegetation.

2. The combined vertical range of the four chief associations (2-5) is less than 4.5 feet (= 1.37 metres). The vertical ranges of the individual species composing an association may vary, thus interfering with the definiteness of the associations. From the physiological (and ultimately, therefore, the distributional) point of view, the vertical ranges of the individual species are of great importance.

3. The greater part of the paper discusses what may be termed "phyto-geological" problems, and deals with the effect of salt marsh plants in modifying and controlling ordinary geological processes.

4. The habits of the plants are discussed, and it is seen that they form an assemblage of extremely effective collectors and binders of silt. In the building of primary marsh, *Glyceria maritima* is the most important pioneer (not *Salicornia* as in some marshes, e.g. Bouche d'Erquy). As the level of the marsh gradually rises, owing to accretion of silt, *Glyceria* is followed by a more or less definite succession of other plants (cf. associations above).

5. The vegetation covering the marsh is never entirely continuous, for from the first certain parts remain bare. These are (1) the channels, by which tidal waters enter and leave the marsh, and (2) the "pans," i.e. shallow depressions with no definite outlets; these remain filled with water after the retreat of spring tides.

6. When primary marsh has been formed, it is subjected to a continual struggle between the agents of erosion and retrogression on the one hand, and those of deposition and consolidation on the other. This struggle results in many changes of a secondary character, the surface relief of the marsh being profoundly modified. The history of these surface changes has been studied mainly by the indirect method of comparison of different stages found on the marsh at the present day, rather than by the direct, but more lengthy, method of following the development from year to year.

7. The sward is exceedingly dense and compact, and its surface has great power of resisting wave attack. As the level of the marsh rises, however, its riverside margin becomes more and more vulnerable, and is constantly undermined by the waves, an erosion escarpment being formed. Thus retrogression occurs along the margin of the marsh, but is compensated by the formation of secondary marsh at a lower level, below the escarpment. The fallen blocks of turf form new centres of colonization, *Glyceria* acting, as usual, as a pioneer in the process of reconstruction.

8. The channels are tidal throughout their entire length, and are usually empty between spring tides. That is, their currents are both reversible and intermittent. A channel may shift its course in much the same way as does a river on land. If for any reason the volume of water is insufficient to keep

a channel permanently open, it may either (1) become blocked at various points, and so be converted into a chain of "channel pans," or (2) be gradually narrowed and finally roofed in, thus becoming subterranean. Both processes are an expression of the tendency of the vegetation to spread on, and consolidate accumulated silt. In general, segmentation into pans usually occurs in shallow channels, while deeper ones tend to become subterranean. Frequently the upper reaches of a channel are converted into pans, while the lower reaches of the same channel become subterranean.

9. Pans may arise in a variety of ways. Four distinct methods were observed on the Dovey marshes. (1) Primary depression pans are formed from hollows into which vegetation cannot spread during the development of primary marsh. (2) Secondary depression pans have a similar origin, but arise on secondary marsh. (3) Channel pans are formed by segmentation of a channel, and (4) Residual pans are bare, depressed spots left during the recolonization of a quiescent pan. No evidence was found that pans ever originate *de novo* on a sward-covered surface, as suggested by Warming.

10. When once formed, pans are subject to considerable modification. They may either increase or diminish in size, alter their shapes, change their positions, or even disappear altogether.

11. During the active enlargement of pans by erosion, they exhibit a tendency to become circular (especially on sandy marsh), owing to eddies similar to those which produce "pot holes" in a rocky river bed. Enlarging pans frequently coalesce and form compound pans.

12. As a rule pans are remarkably persistent, but under certain circumstances, especially when drainage is established, they may become carpeted by vegetation. When their level is built up to that of the surrounding sward, they disappear altogether.

13. Physiological work is still in its infancy, but there is abundant evidence to show that the vertical distribution of salt marsh plants, as well as their capacity to invade pans, depends largely on the frequency and duration of the periods of submergence and emergence respectively. The nature of the substratum, whether sandy or muddy, is also important.

14. The final section deals briefly with the economic aspect of the marshes.

We wish to express our thanks to Professor O. T. Jones, for kindly reading through the "phyto-geological" portion of this paper; to Mr G. C. Druce, for critically examining and naming several plant specimens, and finally to the Council of the University College of Wales, Aberystwyth, for a grant towards defraying the expense of the plates.

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DESCRIPTION OF PHOTOGRAPHS ON PLATES XII—XVI

Capital letters denote locality, and refer to Fig. 1. Months (in brackets) refer to the time of year when the photographs were taken.

Plate XII.

- Phot. 1. General view of marsh towards head of estuary, taken from hill above D. Note the raised strip of land immediately bordering on river, with a lower strip, occupied by **Armerietum** (now submerged), behind it. (August.)
- Phot. 2. Sward (mainly **Lower Festucetum**) with deep pans. *Armeria* in flower. Between C and D. (June.)
- Phot. 3. **Juncetum** and sward, near A. (July.)
- Phot. 4. Unusually abrupt lines of demarcation between the three sward zones (**Glycerietum**, **Armerietum** and **Festucetum**). On further side of stream only the two lower zones are represented. Mouth of tributary stream west of B. (July.)

Plate XIII.

- Phot. 5. Early stage in primary building of marsh. Note thin growth of *Glyceria* on silt, and raised hummocks (darker) with *Armeria*: also incipient primary channels. At C, looking towards breakwater (B), which forms horizon on right. (July.)
- Phot. 6. Somewhat later stage of marsh building. Carpet of *Glyceria* (light) denser and more continuous. Hummocks with *Armeria*, etc. (darker) larger and more numerous. An incipient primary depression pan is seen in foreground (see Fig. 7 II), and further away a channel crossing sward from left to right. At C. (August.)
- Phot. 7. Channel, fringed mainly by *Glyceria*, on developing primary marsh. The outer sides of bends show erosion, while *Glyceria* is extending on silt deposited on inner sides. This accentuates the winding of channel. At C. (August.)
- Phot. 8. **Salicornietum**, with temporary depression pan. Note sun cracks. Between River Leri and A. (August.)

Plate XIV.

- Phot. 9. Retrogression at edge of secondary marsh. Two parallel erosion escarpments are seen, one at the edge, the other further back. *Armeria* in flower. Between C and D. (June.)
- Phot. 10. Marginal erosion and formation of secondary marsh, by recolonization from fallen turfs. *Glyceria* is the pioneer. Sandy marsh at A. (July.)
- Phot. 11. Formation of secondary marsh. *Glyceria* spreading from fallen turfs at edge of marsh. The hollows containing water may become secondary depression pans. Between C and D. (June.)
- Phot. 12. Escarpment with secondary marsh formed at lower level. *Armeria* in full flower. Between C and D. (June.)



Phot. 1



Phot. 2



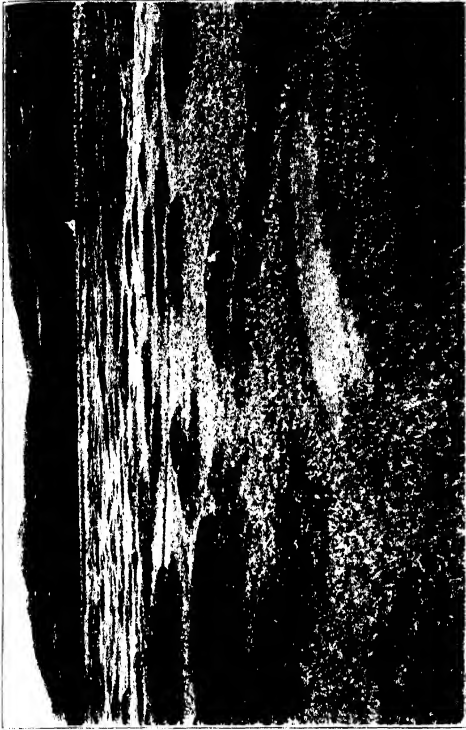
R. H. 1, phot.

Phot. 3.



Phot. 4

YAPP, JOHNS AND JONES—THE SALT MARSHES OF THE DOVEY ESTUARY (pp. 65—102).



Phot. 6



Phot. 8



Phot. 5



Phot. 7

YAPP, JOHNS AND JONES—THE SALT MARSHES OF THE DOVEY ESTUARY (pp. 65—102).

R. H. V. phot.



Phot. 10



Phot. 12



Phot. 9



Phot. 11

R. H. V. photo.

YAPP, JOHNS AND JONES—THE SALT MARSHES OF THE DOVEY ESTUARY (pp. 65—102).



Phot. 14



Phot. 16



Phot. 13



R. H. Y. 1917.

Phot. 15

YAPP, JOHNS AND JONES—THE SALT MARSHES OF THE DOVEY ESTUARY (pp. 65—103).



Phot. 17



Phot. 18



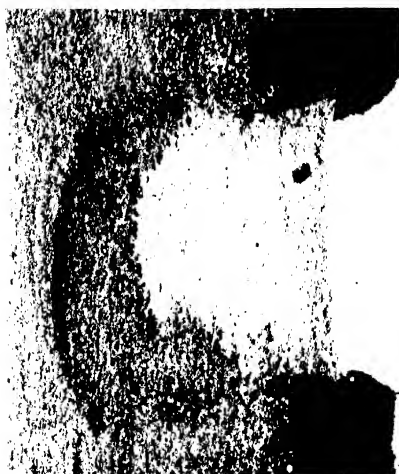
Phot. 19



Phot. 20



Phot. 21



Phot. 22

YAPP, JOHNS AND JONES—THE SALT MARSHES OF THE DOVEY ESTUARY (pp. 65—103).

Plate XV.

- Phot. 13. Early stage in formation of subterranean channel. *Glyceria* invading sides of channel. Near A. (September.)
- Phot. 14. Later stage of ditto. Channel is now very narrow, owing to continued accumulation of silt, and its consolidation by *Glyceria* and other plants. The former banks of the channel are still clearly visible. Near A. (September.)
- Phot. 15. A still later stage. Several "land bridges" are seen, roofing in parts of a channel. Note the drained pan, which is carpeted by *Glyceria*, etc., except for two spots (potential "residual pans"). Near A. (September.)
- Phot. 16. Early stage in formation of "channel pans." A channel is blocked by silt (with *Glyceria*) at its junction with a small tributary channel (also shown in Fig. 7 III). At C. (July.)

Plate XVI.

- Phot. 17. Later stage in development of a chain of channel pans. The former limits of channel are still visible. At A. (August.)
- Phot. 18. A chain of old channel pans. The sward surrounding the pans has been built up to the general marsh level, so that position is the only indication of the method of origin. At D. (August.)
- Phot. 19. A system of actively enlarging pans which will ultimately give rise to one large compound pan. Note tendency to form circular pans. The same pan system is shown in Fig. 9. At A. (August.)
- Phot. 20. Large compound pan. The rounded outlines of the formerly separate contributing pans are clearly seen. Note salt efflorescence on bare floor of pan; also "islands" on left of pan. Compare earlier stage shown in Phot. 19, where an "island" is in process of formation. Contrast the shallow pans on sandy marsh (at A) seen here and in Phot. 19, etc., with the deeper pans on more muddy marsh (Phot. 2, 21, etc.). (August.)
- Phot. 21. Large pan, possibly compound in origin, near D. Note the smooth, rounded, overhanging sides characteristic of "overgrowth," and contrast with Phot. 18, 19, 20, etc. (August.)
- Phot. 22. Pan, near A, which has been drained by connecting up with a channel at a lower level. Invasion by *Glyceria* is proceeding regularly from distal end, so probably no "residual pans" will be left, cf. Phot. 15. (July.)

ON THE ÉCOLOGY OF THE VEGETATION OF BRECKLAND.

BY E. PICKWORTH FARROW.

IV. EXPERIMENTS MAINLY RELATING TO THE AVAILABLE WATER SUPPLY.

(With Plates XVII and XVIII and one Figure in the Text.)

When the great influence of rabbits upon the vegetation of the Breckland heaths had been ascertained¹ it became clear that unless the rabbit pressure were removed from an area the rabbits would spoil the results of any detailed experiments upon other factors.

A large quadrat, 3 metres square, in the middle of the degenerate grass heath association was therefore carefully fenced off from rabbit attack by wire netting (on April 5th, 1914). The rabbit-proof wire netting of this large quadrat projects 4 feet above the surface of the soil and is inclined slightly outwards (see Pl. XVII, Photo. 1, and Fig. 1, p. 107). The netting was let down several feet into the sandy soil and the bottom edge was bent sharply outwards, so that if any rabbits tried to burrow down immediately outside the netting they would eventually encounter netting on two sides and would probably desist from further effort.

After the discovery of the great effects of the rabbits on the vegetation it was thought that the poorness of the vegetation of the grass heaths was probably chiefly due to the rabbits, and it was expected that when all the rabbits were removed from an area the associated vegetation would quickly become much more luxuriant.

This however proved not to be the case during the first year. The vegetative portions of the plants inside the large rabbit-proof quadrat were but little more luxuriant, and only slightly taller, than those of the plants on the exposed grass heath, the chief difference being that the sheltered area bore a far greater number of inflorescences.

It thus appeared that the growth of the vegetation on this area was probably being severely² limited by some other factor or factors than

¹ Part III. This JOURNAL, 5, pp. 1-18.

² The word "severe" is used in this connexion to mean that the rate of growth is very much less than it would be if the value of the factor were so increased that it ceased to be a limiting factor: or, to put the matter another way, that its value would have to be greatly increased before the factor ceased to limit the rate of growth. The extent of the "severity" at any instant of time would be measured by the difference between the rate of growth if the value of the factor in question were so increased that it ceased to be a limiting factor, and the otherwise normal rate of growth; and the total effect of the severity during any given period of time would be measured by the area enclosed between the graphs of these two functions.

rabbit attack. It appeared that the rabbit attack probably tended to control the *luxuriance* of the vegetation (i.e. the amount of vegetative substance present), tending to keep it down to a certain small amount, while it also appeared that the *rate of growth* of the vegetation was probably being severely controlled by some other factor¹.

General observations upon the usually greater luxuriance of the vegetation in the valleys when protected from rabbit attack and where the soil is much damper—although the peaty soil of some of the valleys of course introduces other edaphic conditions—compared with the lack of luxuriance of the vegetation on the upper areas when protected from rabbit attack, and general considerations upon the porous nature of the sandy soil of the upper areas and the low rainfall of the district, made it appear that the available water-supply might be an important limiting factor to the growth of the vegetation on the upper areas of the district.

It was at first intended to estimate the holard and chresard of the soils on the upper areas and of the soils in the valleys by one of the usual laboratory methods. There are however two serious objections to such methods when employed as a means of determining the actual factors at work on natural vegetation. In the first place the sources of error due to the fluctuating water content of different layers and of adjacent masses of soil, to determinations taken at different periods after rainfall, etc., are numerous. And even if these sources of error are recognised and corrected the supposed information as to the ecological factor at work would depend upon the assumption that the observed differences in the vegetation are due to water supply, whereas they might in reality be due to some wholly different factor, such as variation in some mineral constituent of the soil.

It thus appeared that actual experimentation by alteration of the existing water supply of the vegetation itself on the upper areas would be a far sounder method of determining whether and to what extent available water supply was an effective limiting factor to the growth of the vegetation on these grass heaths than mere direct determinations of water content.

¹ The relation between luxuriance, rate of growth and rate at which the rabbits eat the vegetation may be expressed mathematically as follows:

$$\begin{array}{ll} \text{If} & \text{Rate of growth of the vegetation} = V, \\ & \text{Rate at which the rabbits eat the vegetation} = R, \\ \text{and} & \text{Amount of vegetation existing at any time, i.e. luxuriance} = L. \\ \text{Then} & \text{Rate of increase of } L \text{ at time } t = \frac{dL}{dt} = V - R. \end{array}$$

For the condition of equilibrium to be stable the condition required is that if L is greater than its equilibrium value the sign of $\frac{dL}{dt}$ must be negative, and where L_0 is the initial value the value of L after a finite time t will be

$$L_0 + \int_0^t (V - R) dt.$$

WATER DRIP AND MANURING EXPERIMENT.

The method it was eventually decided to employ in this instance was to increase artificially the available water supply at a certain spot by means of a water drip from a water-containing vessel; and if the actual growth of the vegetation were increased at this spot it would be established that under the natural conditions the available water supply was an effective limiting factor to the growth of the vegetation on the heath¹. Further the magnitude of the observed effect might give some indication of the extent of its actual limiting influence under the natural ecological conditions. A barrel fitted with an ordinary wooden tap proved quite a satisfactory water container provided the tap was protected from the heat of the sun.

It was also thought that the available supply of some manurial constituent might possibly be an effective limiting factor to the growth of the vegetation. A metre quadrat was therefore heavily manured with farm-yard manure to see if this resulted in an increased growth of the vegetation under the dry conditions. In order to ascertain any combined effects, in addition to the separate effects, of increased water supply and increased supply of manurial constituents, the water drip was arranged so as to add to the water supply at a point half way along the line separating a manured quadrat from an unmanured quadrat (see diagram, Fig. 1). The water was arranged to drip fairly profusely in order that the water supply should cease entirely to be a limiting factor immediately around the drip; and since it was desired that any result should allow for the total time as well as for the absolute extent to which the available water supply might be a limiting factor to the growth of the vegetation and should indicate the product of these two quantities, the water was arranged to drip continuously.

After the water drip had been working for about a week, it was noticed that the grass for a radius of about 20 cms. all around it was slightly taller than the grass elsewhere (see Fig. 1). The increased height was at first about uniform over this circular area around the water drip and fell off very rapidly at the edge of the circle. As time went on however the grass near the centre of the circle close to the actual drip increased in height more quickly than that near the outer edge of the—at first uniform—irrigated circle, and eventually the vegetation immediately around the drip became very much taller and more luxuriant than the vegetation elsewhere (see Pl. XVII, Photos. 1 and 2).

As a result of this experiment there is no doubt whatever that the available water supply is a factor which severely limits the growth of the natural vegetation of this grass heath, and the very great importance in ecology of

¹ Cf. Blackman, F. F., and Smith, A. M., "Experimental Researches on Vegetable Assimilation and Respiration IX," *Proceedings of the Royal Society, B*, vol. 33, 1911.

the conception of limiting or controlling factors is strikingly illustrated. The result of this irrigation experiment emphasises the advisability of doing everything possible to conserve the natural water supply if ever these heaths are reclaimed for the purpose of arable cultivation.

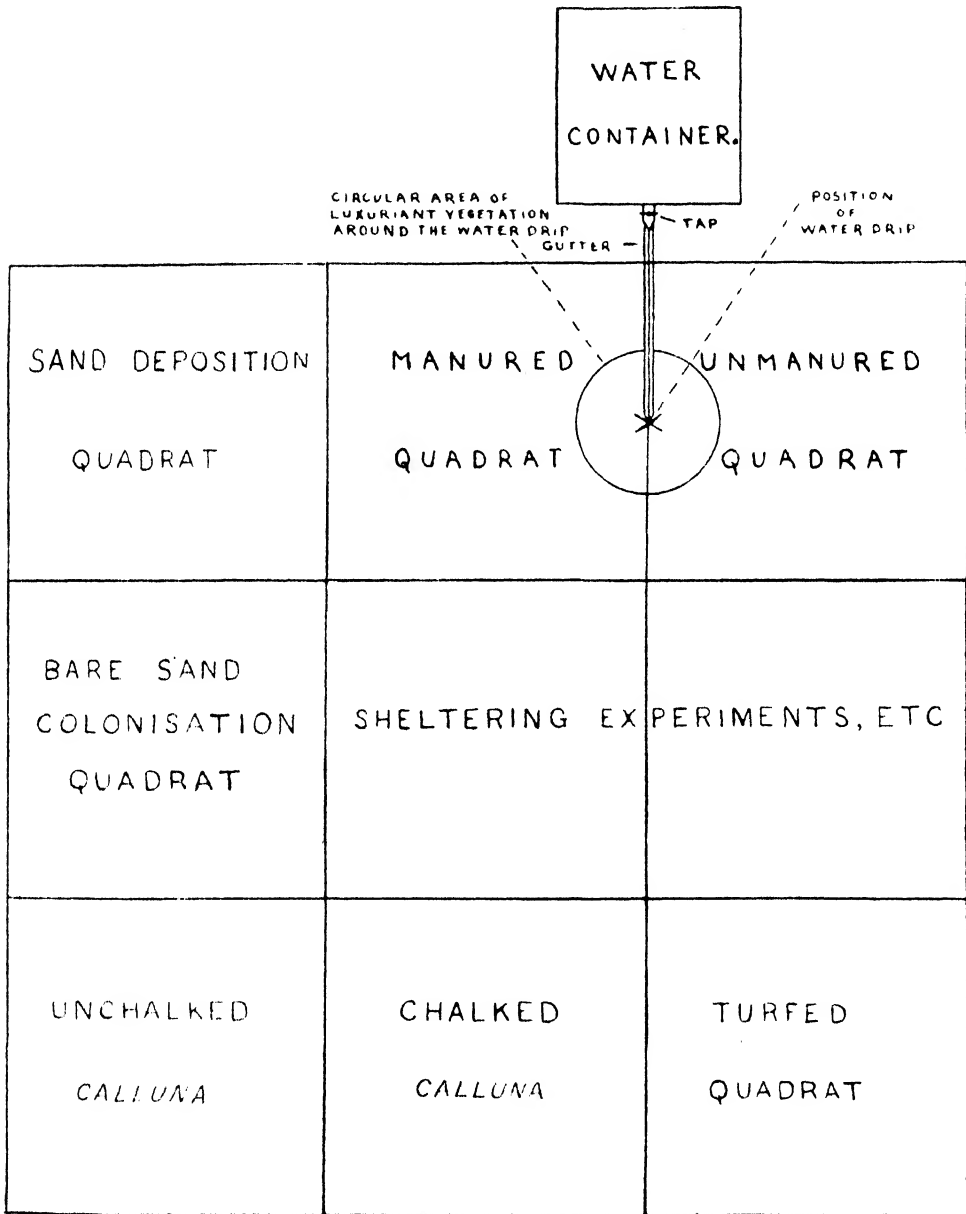


FIG. 1. Diagram showing arrangement of the experimental quadrats, etc. inside the large rabbit-proof enclosure. Each minor quadrat is 1 metre square. See text for description of the water drip, of the manured and unmanured quadrats, and of the sheltering experiments. The other experimental quadrats will be dealt with in subsequent parts.

It has already been mentioned that the irrigation at first produced a circular patch of vegetation of a uniformly increased height which fell off rapidly at the edges, but that afterwards the more central portions grew taller than the outer portions of the at first uniform patch. The probable explanation of this difference is that at first the whole of the vegetation of the uniform patch received water as quickly as it could be utilised by increased transpiration and growth, but that, as the central plants grew taller and taller, having the first access to the increased water supply, they were gradually able to use a greater and greater proportion of it, so that there was then less left for the outer plants, which consequently could not then grow as fast as the central portions, although they did so at first.

It has also been mentioned that a quadrat on one side of the water drip was heavily manured whilst a quadrat on the other side of the water drip was left unmanured. Soon after the experiment had been started, it was noticed that the vegetation of the manured quadrat was slightly more luxuriant than that of the unmanured quadrat (see Pl. XVII, Phot. 2, and Fig. 1, p. 107). (This also applied to the vegetation of a manured quadrat which was exposed to rabbit attack outside the large rabbit-proof quadrat, but in this case the rabbits quickly nibbled off the slightly more luxuriant vegetation on the manured area, and soon brought it down to the low constant level of the general vegetation of the exposed grass heath.)

With regard to the manured quadrat protected from rabbit attack one was rather surprised at first that the addition of the manure alone produced any increase in the luxuriance, since the water drip experiment was showing that the available water supply itself was such a severe (i.e. powerful and long continued) limiting or controlling factor to the growth of the vegetation. The explanation no doubt is that in nature there are a number of different limiting factors operating at different times. Probably in this special case for instance, after rain the available water supply ceases for a time to be the limiting factor to the growth of the vegetation and something else becomes the limiting factor—probably in this case chiefly the available supply of potassium. It is hoped to test this latter supposition later on by the experimental addition of potassium salts without placing faith in laboratory determinations of so-called “available” potassium. In this connexion the greater height of the tied-up sheaf of grass on the manured side of the water drip as compared with that on the unmanured side should be noted (Pl. XVII, Phot. 2. A 30 cm. rule is seen in the photograph).

Length of Leaf Blades of *Agrostis vulgaris* in cms.

	Maximum	Average	Average Increase
1. Untreated Area	3	1.5	
2. Manured only	12	9.0	7.5
3. Irrigated only	47	36.0	34.5
4. Manured and irrigated	59	45.0	43.5

From the above figures it will be seen that the water drip alone produced an average increase of 34.5 cms. in the length of the leaf blades of *Agrostis vulgaris* while the addition of manure alone only produced an increase of 7.5 cms. It will thus be seen that it has been experimentally demonstrated that water supply is a far more severe limiting factor to the natural growth of the vegetation on this grass heath than anything which was supplied in the complete general manure.

The vegetation of the irrigated patch consists almost entirely of *Agrostis vulgaris* although on the untouched grass heath *Festuca ovina* is co-dominant with *Agrostis vulgaris*¹. Apparently the alteration of one factor of the environment alone has enabled the *Agrostis* to crowd out the *Festuca*. As the experimental alteration of the water supply alone has enabled the *Agrostis* to become dominant on this dry sandy heath this may rather tend to indicate that the far greater dominance of *Agrostis* on the damper siliceous soils is very likely really largely due to the greater water supply. This matter should however be directly tested experimentally in some way or other and it may justly be hoped that the employment of such experimental methods in ecology will contribute far more materially to the sound advance of ecology than the laboratory determinations and deductive processes which are frequently solely employed. It will be seen later that the incomplete dominance of *Agrostis* on Cavenham Heath is also partly due to the heavy biotic attack on this area.

“EDGE-EFFECT.”

In addition to the luxuriance of the vegetation being greatly increased just around the water drip there is also a strip of vegetation more luxuriant than the general vegetation of the enclosed area just inside the wire netting along the sides of the quadrat (see photographs).

The writer has observed during rain that some of the rain water falling on the sloping wire netting fence tends to be collected by the sloping wire netting, to trickle down it and to be deposited along a line at the bottom of the netting on the surface of the soil: probably the same thing happens with dew. The greater luxuriance of the vegetation just inside the wire netting around the quadrat is thus probably largely due to the netting collecting rain and dew and thus adding to the available water supply of the strip of vegetation just where the netting comes in contact with the soil.

The greater luxuriance of the vegetation just inside the edge of the large rabbit-proof quadrat compared with the central enclosed vegetation is however probably chiefly due to what may be termed an “edge effect.” The original

¹ It will be noticed that the leaf blades of the *Agrostis* on the irrigated patch are badly laid (see Pl. XVII, Photo. 2).

vegetation just outside the quadrat was unavoidably destroyed in the digging necessary to insert the netting in the soil, and in any case the rabbits would keep any external vegetation nibbled down closely to the surface of the soil. The sparse and short external vegetation cannot transpire so much water per unit area of soil as the more luxuriant internal protected vegetation, and the roots of the strip of protected vegetation just inside the wire netting and bordering upon the sparse external vegetation can thus absorb some of the water supply which would otherwise be used up by the latter. This external strip of protected vegetation can thus grow more luxuriantly than the central area of protected vegetation which has to compete for its water supply with equally luxuriant vegetation on all sides¹.

Wooden boarded quadrats have been let into the surface of the soil along one side of the large rabbit-proof quadrat for the purpose of various detailed experiments upon the vegetation, which will be dealt with later. Along the border of one of these, which had been denuded of vegetation, the "edge effect" mentioned above was very strikingly evident.

EFFECT OF WINTER RAINS ON PROTECTED VEGETATION.

It was mentioned on p. 104 that when all the rabbit pressure was removed from the area inside the rabbit-proof enclosure the associated vegetation was expected rapidly to become considerably taller and more luxuriant than the vegetation outside. This however proved not to be the case to any extent during the first year, except just inside the sloping wire netting and of course around the water drip.

Since the experiment upon the available water supply was showing that water supply was severely limiting the growth of the vegetation it was thought that after the following winter rains the protected vegetation would probably become considerably more luxuriant than during the first year of the experiment. This expectation was realised, for in the second year the general protected vegetation inside the large rabbit-proof enclosure was considerably more luxuriant than it was during the first season (compare Photo 3 with Photo 2). *Agrostis vulgaris*, *Festuca ovina*, *Aira praecox*, *Rumex acetosella*, *Carex arenaria* and *Calluna vulgaris* especially became much more luxuriant and flowered much better inside the rabbit-proof enclosure in the second year than during the first year (see Plate XVIII, Photo 3). Outside the enclosure, on the exposed grass heath, no inflorescences of these plants occur except occasional very dwarf ones of *Aira praecox*.

¹ Cf. **Shantz, H. L.**, "Plant Succession on Abandoned Roads in Eastern Colorado." This JOURNAL, 5, p. 25. The larger size and greater luxuriance of plants growing on the edge of areas cleared for crops and the bending of the roots of these plants under the open ground, i.e. in the direction of greater water supply, are very strikingly seen everywhere in the short-grass vegetation of the dry Colorado Great Plains (Editor, *Journal of Ecology*).

Galium saxatile is seen in Photo 3 flowering luxuriantly in the S.W. corner of the quadrat and also a short distance along on the right-hand side. Outside this quadrat on the general exposed surface of the grass heath no *Galium saxatile* flowers were to be seen. On the exposed grass heath the rabbits entirely prevent the flowering of this plant as well as of the species previously mentioned, viz.: *Campanula rotundifolia*, *Sedum acre*, *Rumex acetosella*, *Galium verum*, *Calluna vulgaris*, *Festuca ovina* and *Agrostis vulgaris*¹.

OTHER EXPERIMENTS AND OBSERVATIONS.

Later on in the second year the *Agrostis vulgaris* on the manured quadrat produced a very large number of inflorescences in a dense mass and of an average height of 35 cms. These inflorescences were enormously more numerous and of far greater height on the manured quadrat than elsewhere, with the result that the manured quadrat presented a very striking contrast to the rest of the enclosure. This striking effect of the manure upon the production of inflorescences by *Agrostis* did not occur during the first year.

Shortly after the large rabbit-proof quadrat had been constructed a small wooden quadrat was pegged down on the enclosed grass heath in order to shelter partially an area of the vegetation from sun and wind, and small quadrats with glass sides were also pegged down in order to shelter areas from the wind while leaving them exposed to the sun. The small glass quadrats were made very shallow so that they should not give any results through trapping radiant heat. Small wooden boards and glass sheets were also fixed at right angles on the grass heath in order to shelter areas from wind and sun and from wind only respectively. A small sheet of glass was laid on the surface of the grass heath and a straw mulch was pegged down on another area of the surface. In addition a small glass greenhouse with sloping sides and open ends was constructed with two sheets of glass. Some of these devices can be seen in Photos 1, 2 and 3. None of these arrangements gave any very definite result during the first year except that the vegetation under the piece of glass which was laid on the surface of the grass heath very quickly died, and that the vegetation just behind the northern side of the board which ran from east to west and which was partly sheltered from the sun was appreciably more luxuriant than the general enclosed vegetation. In the spring of the second year, however, the vegetation under the small glass greenhouse consisted entirely of a dense mass of *Galium saxatile* which flowered very vigorously and completely filled the glass shaded space. In the second year *Poa pratensis* appeared inside the large rabbit proof enclosure near the N.W. corner and flowered vigorously. This plant had not previously been noticed on Cavenham Heath and it is not known

¹ See Part III. This JOURNAL, 5, No. 1, p. 3.

how or why it has appeared. Possibly some of the seeds may have been introduced with the wire netting or with the stakes.

During the first year *Festuca ovina* was co-dominant with *Agrostis vulgaris* in the grass heath vegetation inside the large enclosure, but during the second year *Agrostis vulgaris* was far more prevalent than *Festuca ovina*. Hence it appears that *Agrostis vulgaris* suffers more from heavy rabbit attack than does *Festuca ovina*. This is probably largely because the *Agrostis* leaves tend to grow taller than the *Festuca* leaves and are thus more readily eaten and suffer more from the rabbit attack, but when the heavy rabbit pressure is removed the taller growing *Agrostis* leaves are able to smother the more dwarf *Festuca* leaves¹.

During the second year as well as during the first year the vegetation just inside the sloping wire netting was considerably more luxuriant than the general enclosed vegetation. The difference in the luxuriance of the protected vegetation near the bottom of the wire netting and the general central internal protected vegetation in the second year can be seen in Plate XVIII Photo. 3, in which *Agrostis vulgaris*, *Festuca ovina*, *Aira praecox*, *Rumex acetosella*, *Galium saxatile*, *Luzula campestris*, *Calluna vulgaris*, and *Carex arenaria* are growing and flowering vigorously.

Very vigorous and luxuriant young flowering *Calluna* stems growing on the protected side near the bottom of the wire netting in the second year are especially well seen in Photo. 4. The young *Calluna* stems in this position have grown over 40 cms. high in a little over a year, whilst outside the rabbit-proof enclosure any *Calluna* stems are eaten down by the rabbits almost to the level of the sandy soil and are entirely prevented from flowering.

The luxuriance of the protected vegetation seen in the last photograph is partly due to the watering effect of the sloping wire netting and to the previously mentioned edge effect, but if this luxuriant vegetation were exposed to the rabbit attack it would of course very quickly be eaten down to the low constant level of the very dwarf general vegetation of the exposed grass heath on the distant side of the netting.

The *Carex arenaria* inside the rabbit-proof enclosure is growing more vigorously and taller than the grasses now that it has been protected from the heavy rabbit attack. Vigorous leaf blades of *Carex arenaria* can be seen in Photo. 4 associated with the vigorous flowering young *Calluna* stems. If the vegetation inside the large rabbit-proof enclosure were subjected to a certain small constant intensity of rabbit attack probably the *Carex arenaria* inside the enclosure would eventually dominate the *Calluna*, but as the vegetation inside the enclosure has been *entirely* cut off from the rabbit attack, the *Calluna* inside the enclosure will probably dominate all the *Carex* after the latter has dominated the grass heath², and eventually the

¹ See Part III, 5, No. 1, pp. 3 and 15.

² See Part III, 5, No. 1, p. 15.



PHOTO. 1. LARGE EXPERIMENTAL QUADRAT (3 METRES SIDE), FENCED FROM RABBIT ATTACK BY WIRE NETTING AND SITUATED ON THE RABBIT EATEN GRASS HEATH ASSOCIATION. Various experiments have been made upon the protected vegetation inside and the results are described in the text. (Cf. Fig. 1, p. 107.) This enclosure was laid out and fenced in April, 1914 and the photograph taken in August of the same year.

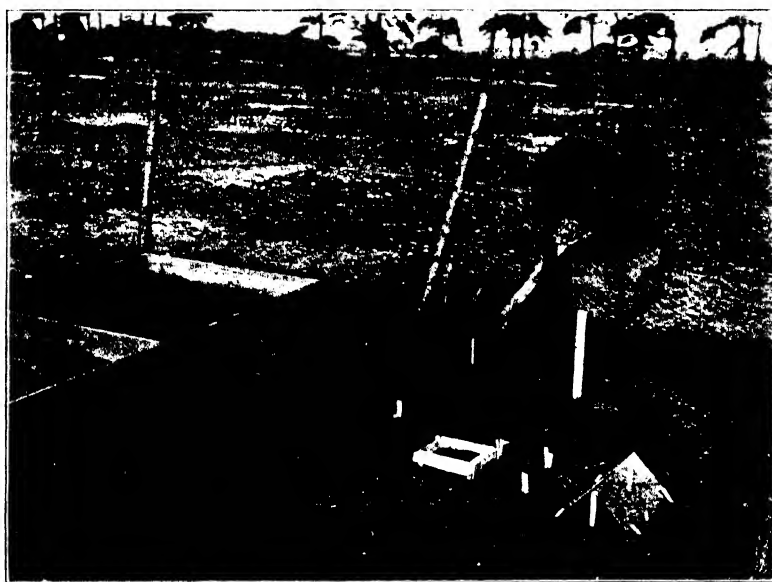


PHOTO. 2. LIMITING FACTOR EXPERIMENT ON THE AVAILABLE WATER SUPPLY OF THE PROTECTED GRASS HEATH VEGETATION INSIDE THE LARGE RABBIT-PROOF ENCLOSURE. The continuous water drip from the barrel resulted in greatly increased height and luxuriance of the vegetation immediately around the drip, thus definitely proving that under the natural conditions the deficient water supply is a severe limiting factor to growth (p. 106). The increased luxuriance of the vegetation on the manured quadrat between the drip area and the boarded quadrat on the left can also be seen (p. 108). Note too the increased luxuriance along the base of the wire netting (cf. Photos 1, 3 and 4). A 30 cm. rule is seen on the right of the drip area. The small wooden and glass quadrats and small "greenhouse" referred to in the text (p. 111) can also be seen in the photograph. Photographed August 1914.

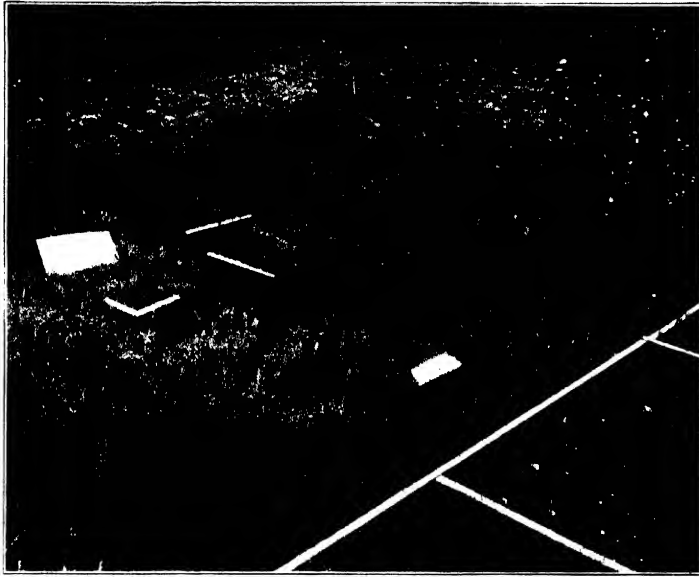


Photo. 3. LARGE RABBIT-PROOF QUADRAT IN SPRING OF 1915. SECOND YEAR OF EXPERIMENT SHOWING THE GREATER LUXURIANCE OF THE ENCLOSED VEGETATION AFTER THE WINTER RAINS (p. 110). Note the extra luxuriance of the vegetation along the base of the wire netting (p. 109). *Galium saxatile* is seen in full flower in the S.W. corner. No inflorescences occur on the exposed grass heath outside the enclosure (p. 111). Photographed June 1915.



Photo. 4. YOUNG *CALLUNA* SHOOTS GROWING AND FLOWERING VIGOROUSLY INSIDE THE LARGE RABBIT-PROOF QUADRAT IN AUTUMN OF SECOND YEAR. Some of these have grown over 40 cms. high in a little over a year now that they are protected from rabbits and under the influence of increased water supply available along the base of the netting. Photographed August 1915.



whole of the enclosure will probably become dominated by healthy *Calluna* heath while the whole of the surrounding area becomes typical pure grass heath.

If the seeds of appropriate trees became deposited amongst the resulting *Calluna* on the protected area these trees would probably eventually dominate the *Calluna* on this area, and if the enclosed area were big enough a small patch of woodland surrounded on all sides by grass heath would ultimately be produced solely owing to the protection of this patch of ground from rabbit attack.

The exact details of the successive developmental phases of the progressive succession on this enclosed protected area inside the large rabbit-proof quadrat, from grass heath to *Calluna* heath and eventually to woodland, owing to the protection of this particular area from rabbit attack, will probably form a very interesting subject of observation.

NOTICE OF PUBLICATION ON FOREIGN VEGETATION

Braun, Josias. "Les Cévennes Méridionales (Massif de l'Aigoual), Étude Phytogéographique" [Études sur la Végétation Méditerranéenne I.]. Genève, 1915, pp. 207.

The *massif* of Mount Aigoual is a classical locality for the botanist, and has been the scene of "herborisations" since the sixteenth century. In recent years its vegetation has formed the subject of much study by Professor Flahault of Montpellier and his pupils. In 1903 a botanical garden¹—L'Hort de Dieu—was established 800 feet below the summit of the Aigoual (5093 feet), and to this Professor Flahault has given unwearying devotion. The memoir here noticed gives a systematic account of the plant communities (*groupements végétaux*) of the *massif*, as well as a description of the geography and climate.

Situation and Climate. The Cevennes, limiting the plains of Languedoc to the north, form a natural barrier between the Mediterranean vegetation and that of central and western France. The actual watershed between the Mediterranean and the Atlantic passes near the summit of the Aigoual *massif*. The climate of the upper regions is of course much wetter than that of the Mediterranean coast, the summit of the Aigoual itself receiving 2175 mm. of annual rainfall against 626 mm. at Palavas and 745 mm. at Montpellier. The most important differentiating factor is however the seasonal distribution of the rainfall in the Cevennes. 42 per cent. of the annual rain falls in the last three months of the year, while only 28 per cent. is received in the five months from April to August inclusive, and only 7 per cent. during July and August. This dry summer accounts for the strongly xerophilous vegetation of a region which receives the highest atmospheric precipitation in France. The author points out that Vallerangue and Le Vigan in the valleys of the Cevennes receive nearly three times as much rain as Belgium and yet the character of the Belgian flora is far more hygrophilous. Hence the ascent high into the

¹ A brief sketch of this garden was given by Mr Macgregor Skene, *New Phytologist*, **10**, 1911, p. 64, under the title "An Ecologist's Garden."

Cevennes of such characteristic Mediterranean plants, with coriaceous, strongly cutinised leaves, as *Quercus ilex*, *Arbutus*, *Phillyrea*, *Cistus*, *Smilax aspera* and *Rhamnus alaternus*. On the upper peneplain and on the slopes towards the Atlantic the distribution of rainfall resembles that of western and central France, the summer drought being less marked: correspondingly the Mediterranean types are almost wholly absent. The dominant wind is the dry and cold *bise* from the north-west. This plunges into the southern valleys of the Cevennes and debouches with fury on the littoral as the well-known *mistral*. The *marin* or *aulan* is the southern and south-eastern wind laden with moisture from the Mediterranean and this brings most of the rain, while the less frequent westerly *aouro basse* or *traverse* brings fine and persistent rain from the Atlantic, but its effect does not cross the ridge. The author gives many valuable data on rainfall, temperature and wind.

Ecological concepts. The author takes the *association* as the fundamental unit. He minimises the importance of *dominants* as often ubiquitous, and lays stress on *constants* but particularly on *characteristics* as the most precise expression of the ecology of a community. Careful statistics give the constants, but observation alone (aided by experience) reveals the characteristic species, whose presence marks, according to the author, the more or less durable state of equilibrium between a community and its environment attained by the well defined fully evolved association. He insists on the importance of the geographical and genetic side of the study of associations. The *formation* he takes as independent of all geographical and historical considerations, "resting solely on the ecological principle," and (with Pavillard) denies the "genus-species" relationship between formation and association stated by the reporters (Flahault and Schröter) to the Brussels Congress of 1910. Consequently the author uses the term "groupe d'associations" for the unit of higher grade than the association. Within the association he distinguishes the *sub-association* (differing from the typical association by the absence of *special* characteristic species). The author adopts Raunkiaer's "spectrum" of biological forms but considers it not wholly satisfactory on the ground that the best bud protection is illusory if a plant begins its active growth at the outset of or during the unfavourable season, which may as well be a hot dry summer as the winter; and that nanism does not necessarily afford the best protection against extreme conditions, since temperatures are often more extreme on the ground than at a little distance above. The whole of the author's discussion of concepts is perspicacious and valuable. He clearly shows the influence of what may be called the floristic school of ecologists.

Systematic description. Sixteen groups of associations are described, some characterised by the edaphic habitat, others by the dominant plant forms. Each is described as of the "type" of a characteristic species, which may or may not be a dominant. Many of the associations described are semi-natural, i.e. they owe their existence to felling, grazing, irrigation, etc. Sheep grazing has had a very destructive effect in the upper regions.

The altitudinal stages of vegetation are represented by that of *Quercus ilex* (up to 600 m.), of *Q. sessiliflora* (600 to 1050 m.) and of *Fagus* (1050 m. to the summits). The last differs markedly in character and climate from the two lower stages. A great number of species do not descend below its lower limit, and outside the beechwoods themselves (which have been largely destroyed though active afforestation is now proceeding) such types as *Calluna*, *Genista pilosa*, *Deschampsia flexuosa*, *Nardus*, *Festuca spadicea* and *Agrostis vulgaris* dominate the communities. The beech stage on the Aigoual massif is in fact an islet of northern vegetation corresponding to an almost oceanic climate characterised by a lower temperature and much greater atmospheric moisture, with abundant rain, frequent mists even in July and August and an average of only about a fortnight of drought. The small beech forest of Sainte Baume in Provence on the other side of the Rhone valley, and situated at an even lower elevation on a very steep northerly exposure, is another instance of the same kind.

NOTICES OF PAPERS OF GENERAL ECOLOGICAL BEARING

ALGAL ECOLOGY

Petersen, J. B. "Studier over Danske Aërofile Alger." *Mém. Acad. Roy. Sci. et Lettres d. Danemark*, 7 ser., Sect. Sci., **12**, No. 7, 1915, pp. 272—352. (French résumé, pp. 353—379.)

This—one of the most important contributions on aërophilous Algae that has yet appeared—is a systematic study of the forms encountered in diverse terrestrial habitats in Denmark. In view of the more or less cosmopolitan character of algal societies, a somewhat detailed abstract will not be out of place. The author's work is divided into two sections, one dealing with the Diatomaceae, the other with the Chlorophyceae.

As regards the former, the author arrives at the following general conclusions. There is a definite aerial association of Diatoms, composed largely of species different to those found in aquatic habitats, although a certain number of amphibious forms have been encountered (e.g. *Achnanthes linearis*, *Denticula tenuis*, *Pinnularia intermedia*, *P. subcapitata*, etc.). It is noteworthy that nearly all the aerial Diatoms belong to the Pennatae, subfamily Raphideae, i.e. are forms endowed with the power of movement. It is suggested that this enables them to survive periods of drought, since such forms will be able to seek out regions of greater humidity. All the aerial Diatoms are of small or very small dimensions (the largest being *Hantzschia amphioxys* var. *genuina*, with a length of 80 μ), a fact which is especially apparent when the aërophilous species are compared with the hydrophilous ones of the same genus. It is thought that the customary small size is related to an increased power of withstanding desiccation.

The author gives the following epitome of the distribution of terrestrial Diatoms:

(a) *On granite rocks*: *Eunotia gracilis*, *Navicula contenta* var. *biceps*, *N. mutica* var. *elliptica*, *Melosira dickiei*, *Achnanthes coarctata*, etc.

(b) *On calcareous rocks* (near the sea): *Denticula subtilis*, *Navicula atomus*, *Nitzschia kuetzingiana*, *N. inconspicua*, etc.

(c) *On the soil of cornfields and gardens*: *Achnanthes coarctata*, *Amphora normanii*, *Hantzschia amphioxys*, a considerable number of species of *Navicula* and *Nitzschia*, *Stauroneis agrestis* n. sp., *S. aerophila* n. sp., etc.

(d) *On woodland and forest soils* Diatoms are often absent, especially where there is much decaying foliage or the soil is sandy. The species recorded are: *Navicula fontinalis*, and other species, *Pinnularia borealis*, *P. brebissonii*, etc.

(e) *On the dry soils of heaths, moors, etc.*, Diatoms are absent, but in the swampy regions one encounters *Pinnularia subcapitata*, *P. borealis*, *Eunotia gracilis*, etc.

(f) *On thatched roofs*: a luxuriant Diatom vegetation, composed chiefly of *Hantzschia amphioxys* vars. *genuina* and *xerophila*, *Pinnularia borealis*, *Navicula mutica* vars., *Achnanthes coarctata*.

(g) *On moist walls*: *Hantzschia amphioxys* vars., *Navicula atomus*, *Nitzschia kuetzingiana*.

In the case of the Chlorophyceae, the author divides the aërophilous forms into a number of societies, according to the conditions of humidity. Those exposed to the least desiccation grow directly on the soil or on objects lying on the soil; these receive a certain amount

of moisture from the underlying layers and from the dew deposited at night. The aërophilous forms found on rocks, on the trunks of trees, or on dead wood are exposed to more intense desiccation, which reaches its maximum in the case of those growing on the upper branches and leaves of trees, where the drying effect of the wind is especially felt. From the ecological point of view, therefore, aërophilous Green Algae can be classified as follows:

1. Growing directly on the soil or on objects rising but little above the soil-surface:

(a) On the soil itself: the Green Algae vary according as the soil is acid in its reaction, or alkaline or neutral. In the former case the most characteristic forms are *Zygogonium ericetorum*, *Mesotaenium violascens*, and two species of *Coccomyxa*, whilst neutral or alkaline soils are always inhabited by *Mesotaenium macrococcum*, and by species of *Hormidium* and *Vaucheria*. Species of *Prasiola* are especially found in localities rich in nitrogenous matter. All such forms growing directly on the soil appear only to prosper where there is not much competition with other vegetation.

(b) On rock-surfaces (near the sea): on granite rocks, where the usual covering of Lichens is absent, the author found *Mesotaenium chlamydosporum*, *Cylindrocystis brebissonii*, *Pleurococcus* sp., *Coccomyxa dispar*, *C. naegeliana*, etc. According to him poor illumination, excessive humidity, and the effect of adjacent towns on the atmosphere are the essential conditions favouring Algae to the exclusion of Lichens in such habitats. On calcareous rocks the author found *Coccomyxa olivacea* n. sp., *Trentepohlia aurea* and Cyanophyceae.

(c) On thatched roofs, which are regarded as presenting similar conditions of humidity: *Cystococcus humicola*, *Dactylococcus bicaudatus*, *Hormidium flaccidum*, *Mesotaenium* spp., *Pleurococcus* spp., *Prasiola* spp., *Stichococcus bacillaris*, *Trochiscia hirta*, and Cyanophyceae.

2. Growing at a slight distance ($\frac{1}{2}$ metre at the most) above the soil, so that moisture can be derived from the latter by capillarity, as well as from dew:

(a) On stony substrata, a distinction being drawn between granite (with sp. of *Pleurococcus*, *Prasiola*, and *Trentepohlia*, *Hormidium flaccidum*, etc.) and walls.

(b) On dead wood there is often luxuriant algal growth, consisting in the main of *Coccomyxa dispar*, *C. naegeliana*, *Dactylococcus bicaudatus*, *Stichococcus mirabilis*, *Hormidium flaccidum*, *Prasiola* spp., *Trentepohlia aurea*. At heights exceeding $\frac{1}{2}$ metre, one finds species better able to withstand desiccation, viz. *Pleurococcus vulgaris*, *P. naegeli*, *P. lobatus*, *Trochiscia hirta*, *Chlorella ellipsoidea*, *Stichococcus bacillaris*, *Trentepohlia odorata* var. *umbrina*, etc.

3. Growing at various heights on trees. In many cases Lichens inhabit the trunks and branches so densely that no Algae can prosper, but the latter obtain the upper hand in the interior of dense forests, where the feeble intensity of the light probably interferes with the development of the Lichens, and near villages and small towns. In large towns Algae do not flourish in such situations, probably because of the products of combustion of coal; in Copenhagen only *Pleurococcus lobatus* and *Cystococcus humicola* were observed.

(a) At a height up to $\frac{1}{2}$ metre above the soil, Algae are practically always found, even when the higher levels are occupied by Lichens, the most typical forms being *Pleurococcus* spp., *Stichococcus bacillaris*, *Trochiscia hirta*, *Dactylococcus bicaudatus*, *Hormidium flaccidum*. Such vegetation (together with *Prasiola* spp.) flourishes especially near human habitations.

(b) On the trunks at a height above $\frac{1}{2}$ metre: *Mesotaenium macrococcum*, *M. chlamydosporum*, *Pleurococcus* spp., *Coccomyxa* spp., *Trochiscia hirta*, *T. granulata*, *Cystococcus humicola*, *Chlorella ellipsoidea*, *Hormidium crenulatum*, *Prasiola muralis*, *Trentepohlia* spp., etc. Certain facts seem to indicate that the kind of tree influences to some extent the species of Algae found upon the trunk.

(c) On the ultimate branches and the leaves of trees. No Algae are usually encountered

on the very young shoots, but in the second season *Cystococcus humicola* and *Pleurococcus lobatus*, sometimes together with young individuals of *Trentepohlia*, are found beneath the exfoliating epidermis and in the young lenticels. In the case of Conifers *Pleurococcus lobatus* has even been found on the needles of the more protected branches, but in all other cases the author sought in vain for phyllophilous Algae.

Fritsch, F. E. "The morphology and ecology of an extreme terrestrial form of *Zygnema* (*Zygogonium*) *ericetorum* (Kuetz.), Hansg." *Annals of Botany*, **30**, 1916, pp. 135—149.

The author deals with a form of *Zygnema ericetorum* inhabiting certain bare areas on Hindhead Common in Surrey. As a result of the extremely inhospitable substratum, it is thought, the usual characters of the terrestrial form of this Alga are developed to a very pronounced extent and some of these appear as adaptations to the habitat. The Hindhead Alga may be said to be permanently in the akinete-condition, its cells agreeing in many respects with the resting-cells of other (aquatic) species of *Zygnema*. The outer portion of the wall is strongly thickened and mucilaginous and is shown to play a part in protecting the cells during periods of drought and in bringing about a rapid recovery on the reappearance of favourable conditions. The cells contain numerous fat-globules which form a dense layer just beneath the cell-wall on the commencement of desiccation. Some little time after moistening the dry filaments, the regular peripheral disposition of these globules disappears. The function of the globules is not altogether clear, but their disposition evidently shows a marked response to the varying conditions of the habitat.

Dry filaments of the Alga recover practically instantaneously when placed in water; further, there is no marked difference between the osmotic pressure of moist cells and those subjected to dryness, nor is there a greater percentage of dead cells in filaments that have been kept dry for months than in those that have been in water for the same length of time. All these features are regarded as indicating extreme adaptation to drought.

Griffiths, B. M. "The August Heleoplankton of some North Worcester-shire Pools." *Journ. Linn. Soc., Botany*, **43**, 1916, pp. 423—432.

The author collected Plankton from a number of pools in the Kidderminster district, situated partly in the basin of the Stour and partly in the valley of a small stream flowing into the Severn. The pools showed marked peculiarities in their respective floras and included many forms which are rare in the Plankton of the large lakes. In those through which a considerable stream flows and which are subject to little contamination, Volvocaceae (*Pandorina*, *Eudorina*) are the dominant forms, whilst Spring Grove Upper and Wilden pools, which are supplied respectively by spring and river water, were dominated by Protococcales. Two other pools which are much contaminated harboured *Microcystis aeruginosa* and other Myxophyceae. Peridineae were especially encountered in Stanklin Pool. Only one collection was made from each pool, so that no general conclusions can be drawn.

Baker, S. M. and Bohling, M. H. "On the Brown Seaweeds of the Salt Marsh. Part II. Their Systematic Relationships, Morphology, and Ecology." *Linn. Soc. Journ., Botany*, **43**, 1916, pp. 325—380.

The conspicuous Fucaceous vegetation of the salt-marsh flora is regarded as originating from the attached Fucaceous vegetation of the rocky shore, this being brought about either by direct vegetative budding from detached thallus-fragments or by the modification of young plants germinating on the marsh. The modifications produced by the new conditions are of the same general type in all the five species found on the salt-marsh; these modifications are prevalence of vegetative reproduction, dwarf habit, absence of an

attachment disc, and spirality or curling of the thallus. All of these except the last are also seen in the Fucaceae of the loose-lying formations of the Baltic described by Svedelius. *Pelvetia canaliculata*, *Ascophyllum nodosum*, *Fucus vesiculosus*, and *F. ceranoides* form definite salt-marsh forms; *F. spiralis* is represented on the marsh by var. *nana*, but this is not a distinct salt-marsh variety. Each of the other species undergoes a series of morphological modifications in the transition from rock to salt-marsh, and the adaptational varieties so produced are regarded as ecads (Clements) and are found to be persistent through many vegetative generations. The several marsh-ecads of each species are grouped together under a megecad *limicola*, and a very useful table is given on p. 348 of the paper showing the relationships between the rock and mud forms. All the dwarf spiral forms of *Fucus*, as well as the turf-like and filiform varieties, occurring on our salt-marshes, are referred to the megecad *limicola* of *F. vesiculosus*.

In the second half of the paper the relationship between the peculiar morphological features of the marsh Fucoids and various physical factors is considered. By examining the distribution of the varieties of a single salt-marsh species, in relation to the variations of certain physical factors and by critical examination of the conditions under which exceptional forms are produced, the following conclusions are arrived at. The most striking peculiarities of the salt-marsh forms are due to a direct response to the new physical and chemical conditions of the habitat, degeneration produced by long-continued vegetative reproduction (as held by Svedelius, etc.) being regarded as of less importance.

Dwarf habit is a result of periodic prolonged exposure, which produces a shortening of the thallus, together with decreased access of nutrient salts, leading to attenuation. Curling or spirality is probably due to unequal distribution of water and nutrient salts upon the thallus. Vegetative reproduction is probably favoured by the high humidity (due to evaporation from the wet soil and transpiration of the associated Phanerogams) in the intertidal periods. This prevents the cell-sap from reaching a certain limiting concentration, which is necessary as a stimulus for the production of receptacles.

The Fucaceae play an important part in the economy of the salt-marsh, acting as pioneers after the ground has been raised and to some extent stabilised by filamentous green and blue-green Algae. The phanerogamic halophytes follow very closely, but the Algae persist as an undergrowth, forming an efficient protection for seedlings and a mulch for the adult plants. *F. spiralis* var. *nana* is a characteristic colonist of the mud-banks formed by erosion and may play some part in the arrest of this phenomenon. The zonal distribution of the Fucaceae is maintained on the salt-marsh, but here the determining factor is the number of tides covering a particular level.

Acton, E. "On the structure and origin of *Cladophora* balls." *New Phytologist*, **15**, 1916, pp. 1—10.

Acton, E. "On a new penetrating Alga." *Ibid.* pp. 97—102.

The author describes the structure of "*Cladophora* balls" from Loch Kildona, South Uist, 2—3 cm. in diameter and due to *C. (Aegagropila) holsatica*, Kuetz. The firm outer shell of the hollow balls is about 3 mm. thick and composed of a mass of separate filamentous individuals tightly interlocked by special branches (rhizoids and cirrroids). Injury to the terminal cell of a plant produces active lateral branching and this explains the close texture of the peripheral part. A somewhat detailed account is given of earlier work on the mode of origin of such balls, but no new facts are added.

In the second paper a new Alga (*Gomontia aegagropilae* n. sp.) growing in the walls of many of the dead cells of the *Cladophora* is described. The same Alga was also observed growing underneath the glaze of a pie-dish in which the "*Cladophora*-balls" were kept.

F. E. FRITSCH.

THE ECOLOGICAL SOCIETY OF AMERICA

This Society has been established in the United States as the result of a desire to provide summer field meetings as well as indoor winter meetings for American ecologists and also adequate opportunities for the meeting together of plant and animal ecologists. An informal conference was held at the end of December, 1914, to discuss the idea, and opinion was practically unanimous that the time was ripe for the organization of an Ecological Society. An Organization Committee was then appointed, and a year later the committee reported to a conference at which the Society was inaugurated and a constitution adopted. The President for 1916 was Dr V. E. Shelford, the well-known animal ecologist. For 1917 the officers are: *President*, Ellsworth Huntington, the well-known climatologist; *Vice-President*, Prof. Harshberger; *Secretary-Treasurer*, Dr Forrest Shreve. The subscription is one dollar annually. The membership in March, 1917, was 307, including a few resident in Canada and one or two outside North America. The Society is now publishing a monthly bulletin of information to its members, and the issue of this for March, 1917, is a very useful Handbook recording the ecological work and interests of each member.

Field trips have been made during 1916 at Dismal Swamp (Virginia), at Chicago, and at San Diego (California) where the Summer Meeting was held.

Standing Committees on "Climatic Conditions," on "Soil Temperatures" and on "Fresh Water Fish and Fisheries" have been organized and the two former have already been at work.

MEETING AT NEW YORK CITY, DECEMBER 27-29, 1916

This meeting, which lasted three days, was held under the auspices of the Columbia University and Barnard College, and in affiliation with the American Association for the Advancement of Science. The following abstracts of some of the papers read are reprinted from the official programme. They show the vigorous activity of American ecologists and the wide extension and application of ecological work. It will be noticed that animal ecology occupies a prominent place in the programme.

PAPERS OF GENERAL ECOLOGICAL INTEREST

Stephen A. Forbes, University of Illinois. "The Relations of Ecology and Economic Entomology" (15 min.). Economic entomology deals with the interactions, actual and possible, between insects and man. It is thus a part of ecology, and the methods and principles of ecology are fundamental to it. The various aspects and diversions of ecology are, however, of very unequal importance to economic entomology, some of those which are now most cultivated being the least so. In view of the great number of investigating entomologists, the growing difficulty of their problems, the great and increasing public interest in their work, and its large importance to the public welfare, it would be highly advantageous both to entomology and to ecology if their relations were precisely distinguished and thoroughly worked out. This would be especially helpful to the teacher of economic entomology, whose special courses might well be based on ecological prerequisites. After a brief discussion of the bearings of some diversions of ecology upon economic entomology, the writer proposes the appointment of a committee to draw up a report on this subject for presentation to the Society at its next meeting.

George P. Burns, University of Vermont. "The Interpretation of Meteorological Data in Plant Ecology" (10 min., illustrated). The present tendency among workers in

plant ecology is to study habitats with the aid of instruments with which they attempt to measure the physical factors under which the plants must develop. In some cases standard recording instruments are available to all workers and their data can be compared, but in other cases each has a separate standard and comparison is not possible. For example there can be no more important study than that of evaporation and its correlation with transpiration under a given set of conditions, and yet we find some using atmometers of various colours and shapes, others using the open pan, and still others inventing new types of evaporimeters. The data gathered are often presented to the reader in the form of monthly or seasonal averages. Such data or averages are of little use in the study of physiological activity of plants. Daily or weekly averages only are important, and these only in the occasional periods of extreme conditions. For example the seasonal average of soil temperature in a shaded bed was only 4 degrees F. below that of an adjacent open bed. The study of differences during short periods showed temperature differences as high as 20 degrees F. This has its important ecological bearing when we know that the higher temperatures were close to the optimum for germination of the seed under observation, and helps to explain the fact that 10 times as many seeds germinated in the open bed as in the shaded one. The only way in which the vast amount of meteorological data can be interpreted by the plant ecologist is by the study of the behaviour of his plants under the same conditions as his recording instruments and the correlation of their behaviour with the factors of the habitat. The great number of possible complications which arise when this is attempted suggests the desirability that the ecologists adopt the methods of precision which are required of the present day physiologists.

V. E. Shelford, University of Illinois. "Physiological Problems in the Life-histories of Animals with particular reference to Seasonal Appearance; illustrated by Seasonal Succession of Spiders on a small plot" (15 min., illustrated). The influence of external factors on growth and fecundity. (a) Temperature, failure of van 't Hoff's law in practical work; Krogh's law; zero or threshold of development; the relations of mathematical zeroes to actual ones. (b) Zeroes and velocities relative to factors other than temperature; light and food; (in air) humidity, velocity, carbon dioxide; (in water) alkalinity, acidity, oxygen. The amount of energy expended in development is probably the same for a given species and for all conditions under which development will take place at all. Dormancy in eggs is comparable to that in seeds; dormancy in other stages. The adjustment of the innate rhythms of organisms to the annual climatic cycle; seasonal appearance of animals; succession throughout the season. Different species in the time in the annual climatic cycle at which development begins, in the time of occurrence of dormancy and conditions necessary to break it up, in zero of development, in velocity of development, total energy expended, in development, and in size. The variations in the annual climatic cycle and various responses of plants and animals to them constitute a maze of intricacy for pure science and afford the basis for the serious problems of the agriculturist and aquiculturist relative to both production and pests.

H. L. Shantz and **Raphael Zon**, Federal Department of Agriculture. "A New Classification of the Native Vegetation of the United States into Natural Groups (plant formations)." Accompanied by a map (15 min.). A brief discussion of the basis used in producing the map which illustrates it.

Frederic E. Clements, University of Minnesota. "The Development and Structure of Biotic Communities" (15 min.). The biotic community is regarded as an organic unit comprising all the species of plants and animals at home in a particular habitat. While plants are regarded as exerting the dominant influence in the community, it is recognized that this rôle may sometimes be taken by the animals. The biotic community, or *biome*, is fundamentally controlled by the habitat, and exhibits a corresponding development

and structure. In its development the biotic formation reacts upon the habitat, and thus produces a succession of biomes, comparable in practically all essentials to the succession of plant communities. Every such succession, or *biosere*, terminates regularly in a climax. The bioseres of each climax are either primary or secondary, and these may be further distinguished as hydroseres, xeroseres, etc.

Henry Fox, Bureau of Entomology. "Distribution of Grasshoppers in relation to the Plant Formations of Tidal Marshes" (15 min.). Two general types of tidal marsh are recognizable in Virginia and southern New Jersey, namely, salt marsh characterized by *Spartina stricta* and a saline soil, and estuarine marshes, characterized by *Spartina cynosuroides*, *Scirpus americanus* or *Zizania aquatica* and by fresh or slightly brackish water. Each of these types is bordered by a zone of submaritime vegetation. Both types of tidal marsh and the more clearly defined plant formations of the marginal zone are characterized by the prevalence of certain distinctive types of grasshoppers. Forms like *Orphulella olivacea*, *Cenocephalus spartina*, *C. nigropleuroides*, *Orchelimum fidicinium* and *Neoconocephalus melanorhinus* are characteristic of the *Spartina stricta* formation of true salt marshes. Estuarine marshes contain species of grasshoppers certain of which are more or less strictly limited to their distinctive plant formations, while others are general marsh dwellers. A number of fresh-water marsh dwellers also occur in estuarine marshes.

Robert F. Griggs, Ohio State University. "Notes on the Return of Animal Life to the Katmai District, Alaska" (10 min.). In the course of studies of the revegetation of the district devastated by the eruption of Katmai, under the auspices of the National Geographic Society, some observations have been made on the return of animal life. The striking thing is that predaceous animals are returning before the return of herbivorous types. This is true of both mammals and insects. Bears, foxes, wolverines, wolves, and weasels are common, but there are no caribou, moose, hares, marmots, ground squirrels, nor mice. The area near the volcano was practically devoid of insect life three years after the eruption (1915) but was fairly swarming with insects the year following. Most of these were predaceous, parasitic or coprophilous. The origin of these insects, their breeding places, and the reason for their sudden appearance are mysteries. They were ravenously hungry and many were dying from starvation.

Herbert Osborn, Ohio State University. "Association and Succession in the Meadow Complex with special reference to Insects" (15 min.). Consideration of the ecological associations found in meadows and pastures with mention of the various organisms entering into this complex and with particular consideration of the insect element and its derivation, succession and economic significance.

Frank C. Gates, Carthage College. "The Relation between Evaporation and Plant Succession in a given area" (12 min.). On this subject diametrically opposite interpretations have been given to the mass of data recently gathered in atmometer experimentation. On the one hand, "Successions between associations are not caused by any conditions of evaporation" (Gleason and Gates, *Bot. Gaz.* LIII, 478-491, 1912), and on the other hand, "The decreased rate of evaporation...is the direct cause of succession between different associations" (Fuller, *Bot. Gaz.* LVIII, 193-234, 1914). The data involved are similar. To ascertain which interpretation was valid, atmometer experiments were carried on in connection with the establishment of *Acer saccharum*, *Pinus strobus* and *Pinus resinosa* seedlings in the summer of 1915 and with *Thuja occidentalis* seedlings in the summer of 1916 in the vicinity of the University of Michigan Biological Station at Douglas Lake, Michigan. Sugar maple is characteristic of loamy soil, pines of sandy soil, and white cedar of bogs. Within their soil limitations and with at least the minimum amount of light, these seedlings developed under the entire range of evaporation conditions present in the region.

The maximum recorded weekly rate from the ground layer was 147 c.c. The fundamental feature of succession is a change to a new set of dominant species. This change must be initiated by invaders, under conditions already existing. By the development of such invaders the evaporation from the chamaephytic layer is usually lowered. Thus a change in the rate of evaporation from the chamaephytic layer is a result and not a fundamental cause of succession.

Roland M. Harper, College Point, N.Y. "Some Dynamic Studies of Long Island Vegetation" (10 min.). Most studies of vegetation hitherto have paid little or no attention to its rate of growth, and the amount of food taken from the soil in a year. The writer has determined these factors approximately for several types of herbaceous vegetation on Long Island by cutting measured areas late in the season, weighing them fresh and dry, and then burning the hay and weighing the ash. The results bring out some interesting similarities and differences between different types.

W. A. Cannon, Desert Laboratory. "The Evaluation of the Temperature Factor in Root Growth" (10 min.). The method suggested is based on two series of data, namely, (1) a continuous temperature record, and (2) the hourly rate of root growth, as determined by experiments, for the optimal temperature, a temperature near the minimal, and for two or three temperatures between. The procedure is as follows: a temperature summation is made for the selected temperatures, and by the use of (2) the growth at these temperatures is calculated. The relative effectualness of any temperature, and for the series of temperatures, can be easily calculated. It is the ratio between the expected growth rates, or growth amounts, and the rate or total growth that would be expected at an optimal temperature or for the given number of hours at the optimal temperature. The method is illustrated by a calculation of the relative value of soil temperatures with respect to root growth for Carmel, California and Tucson, Arizona.

Homer E. Chenoweth, Paxton, Ill. "The Reactions of certain Moist Forest Mammals to Air Conditions, and their bearing on Problems of Mammalian Distribution" (15 min.). It is evident to naturalists that mammals select certain local habitats for their chief places of abode, and that their geographic distribution is a function of the distribution of the conditions so selected. In spite of many theories as to factors controlling distribution of mammals there are apparently no experiments showing the factors to which they react in selecting their habitats. The experiments performed show that the moist forest mammals studied avoid air of high evaporating power, due to dryness, rapid movement or high temperature. The negative reactions to air of high temperature which gives the same amount of evaporation as dry air is no sharper than in the case of dry air with no difference in temperature. The experiments indicate that in the case of the mammals studied the rate of evaporation is more important than temperature in determining their movements. Their resistance to water withdrawal is far greater than that of many other animals of the same community.

C. C. Hamilton, Cornell University. "The Reaction of Soil Insects to Gradients of Evaporating Power of Air, Carbon Dioxide, and Ammonia" (15 min.). In studying the reaction of soil insects to gradients of evaporating power of air, carbon dioxide, and ammonia it was noticed that both the larvae and the adults were very sensitive to evaporation. The larvae avoided the dry air the best at temperatures of 20 to 22° C. Increasing the rate of air flow did not affect the larvae as much as either increasing the temperature or decreasing the relative humidity. In those experiments in which the larvae had been subjected to freezing weather for a number of days, the optimum temperature at which they avoided the dry air was lowered from about 22 to 16° C. It was also noticed that larvae collected early in the fall withstood high temperatures better than those collected later. The adults behaved somewhat similarly to the larvae but were more resistant.

Their greater resistance to evaporation and temperature is natural since they are usually found on the surface of the soil or near it, and are thus subjected to higher temperatures and drier air. The increased chitinization of their bodies is also a greater protection against evaporation from the body surface. In the experiments with carbon dioxide both the larvae and the adults selected air containing 5 to 6 per cent. of the gas in preference to air containing higher or lower amounts. On the other hand, neither the larvae nor the adults selected air containing ammonia, although they did not always react advantageously to it. The percentages used, however, were probably considerably larger than those ever encountered in nature.

George N. Wolcott, University of Illinois. "The Influence of Rainfall and some other factors on the Abundance of the Sugar-Cane Moth Stalk Borer (*Diatraea saccharalis*)" (10 min.). Results of several years' observation in Louisiana, Cuba, Jamaica, Trinidad and Barbados, and careful status examination for two years in Porto Rico, show that the abundance of the Sugar-Cane Moth Stalk Borer (*Diatraea saccharalis*) varies inversely with the rainfall. The status examinations of 1914-15 showed nearly 100 per cent. increase in numbers of *Diatraea* in fields where the trash had been burned the previous years, but the results of 1915-16 were not so striking and were negative in a few cases. Cane growing on steep hillsides is usually 100 per cent. infested with the borer.

Frank Smith, University of Illinois. "Correlation of Migratory Flights of Birds with certain Meteorological Conditions." Much of the recent literature on the subject of bird migration tends to minimize the importance of meteorological conditions in determining the times at which the separate flights take place that, in the aggregate, make up the migration movements of birds. Such conclusions may be expected when the data used are chiefly the records of "first seen" by isolated observers who are more or less irregular in their periods of observation. The results of fourteen years of observation of the Spring migration, based on daily records of several observers in the vicinity of Urbana, Illinois, and on bulk movements and disappearances as well as on new arrivals, show conclusively a high degree of correlation between the flights of night migrants in central Illinois and the meteorological conditions involved in the near approach from the west of an area of low barometric pressure with the accompanying south winds which often involve an area extending as far as the Gulf of Mexico.

W. M. Smallwood, Syracuse University. "A Zoological Study of Lake Clear" (15 min.). Lake Clear, Franklin County, N.Y., is at the head-waters of the Saranac Lake system. Two small streams empty into it but most of its water comes from springs. This means that the water is cold even during July and August. A spring on the north shore averages during the summer about 54° F. The lake itself is about 3 miles long and a mile wide with two large bays at the north-west corner and a single much larger one on the western side. The bottom is formed by the intercepting fault valleys at nearly right angles. The greatest depth is where these two valleys cross and is 60 feet. On the north, east and southern half of the western shore, there is a large shallow area mostly composed of sand. On these three areas must grow the vegetation that directly and indirectly is to furnish the food for the fish of the lake. One of the most notable features of this lake is the sparseness of the plants. One can row for half a mile in August along the shore and only see a few small tufts of *Chara*. During the past 20 years a great many fish have been placed in this lake. These belong to the trout family. It is interesting to note that the white fish is the only species that has shown any marked increase in numbers. This is due to the nature of the food of the white fish. They feed largely upon cladocerans, the winter eggs of which seem to be able to pass through the entire digestive canal without being injured. Practically all of the trout examined were parasited, one brook trout having 604 flat worms in the stomach.

James R. Slater, introduced by W. M. Smallwood. "The Seasonal Behaviour of the Urodela of Onondaga County, New York" (10 min.). Specimens of all the species of Urodela which could be found in this county were collected. Most of them were killed and preserved as soon as they were brought to the laboratory, and later their stomach-contents identified. Some were kept alive in the laboratory for breeding purposes; eggs were hatched and larvae reared. Observations were made in the field at night and during the day as to their first appearance in the spring, breeding habits, development etc., and on water temperature and general weather conditions.

Frank Collins Baker, New York State College of Forestry. "The Relation of the Mollusks of Oneida Lake to the Basin of Lower South Bay" (15 min.). Lower South Bay is a shallow body of water about a mile in greatest diameter, and 11 feet in greatest depth. The bottom is sandy, muddy, and bouldery in spots, the deeper parts being more uniformly of mud. Mollusks live on all of these varieties of bottom, certain species, however, occupying one characteristic habitat to the exclusion of other species. Thus there are typical communities such as *Amnicola*, *Sphaerium*, *Lymnaea*, where these genera predominate. In places where the so-called "blanket algae" cover the bottom the mollusks are notably abundant, consisting of the smaller forms—*Amnicola*, *Valvata*, etc., with the young of such mollusks as *Galba*, *Physa*, and *Planorbis*. Mollusks vary with increase in depth, the large heavy snails of *Goniobasis*, *Galba*, *Lymnaea*, and *Physa* occupying the rocky shores to a depth of 2-3 feet and the smaller snails, *Amnicola*, *Valvata*, *Physa* and the small bivalve *Pisidium*, occupying the deeper water. It was noted that in a single genus—*Valvata*—the species *V. Sincera* was characteristic of the deeper water 10-18 feet, while the species *V. tricarinata* was abundant in the shallower water, 3-8 feet. Seasonal changes affect mollusks, *Acella* living in the vegetation of the deeper water during the spring and summer and migrating shoreward in the late summer and fall when it lives attached to submerged vegetation in shallow water. *Lymnaea* also migrates shoreward in late summer and lives among the rocks and boulders bordering the shore. Quantitative studies were made to ascertain the number of mollusks living in a unit area, in this case 10 sq. cm. It was found that molluscan life was notably abundant: for example, on a sandy bottom 92; on a muddy bottom 81; on a stony bottom 70; in algae 90. A pint of algae from a submerged log yielded no less than 1900 individuals.

A. O. Weese, University of New Mexico. "An Experimental Study of the Reactions of the Horned Lizard (*Phrynosoma modestum*).” These studies were conducted with horned lizards from a semi-desert environment near Albuquerque, N.M. With the aid of the gradient apparatus developed by Shelford and described by Shelford and Deere (*Biol. Bull.* xxv. 79-120) the reactions of the animals in gradients of the environmental factors most subject to variation in the natural habitat were determined. The results obtained justify the following general conclusions. (1) The optimum evaporation rate of air for the species lies between 1.5 and 3 c.c. per hour, as measured with a standard atmometer. This is approximately the average evaporation rate of outdoor air in the natural habitat of the species during the normal period of activity. (2) The reaction in an air temperature gradient is definite. A variation in temperature causes also a variation in evaporation, so that a temperature gradient is really a double one. The optimum temperature is in the region of 30° C. when the humidity and rate of flow of the air are such as to produce an evaporation of 3 c.c. per hour, as measured with a standard atmometer. (3) Air humidity, air temperature and air current gradients are all essentially evaporation gradients, and the optimum in each case is a function of the evaporating power of the air. (4) The most definite and clear cut reaction in a gradient shown in this series of experiments is that in the substratum temperature gradient. It is to a great degree, at least, independent of accompanying differences in air temperature and humidity, or at least, the effect of these

variations is overshadowed by the response to the gradient of substratum temperature. The optimum is between 36 and 40 degrees and at the upper limit a definite reaction (burrowing) takes place. This optimum is correlated with the other optima determined, in that the substratum temperature, under the conditions given in (1), is usually from five to ten degrees above that of the air. Surface temperature is evidently of very great importance in determining details of daily and seasonal life, as well as having its accompanying effect on the distribution of the species. (5) The factors having the supreme rôle in determining the seasonal or general distribution of a species are not the same for all species of the same environment, and before definite conclusions can be drawn a careful analysis of the habitat must be made and experimental data must be obtained as to the reaction of the animals in gradients involving the factor capable of variation.

A. G. Huntsman, Atlantic Biological Station. "Factors in the Distribution of certain Chaetognaths" (15 min.). *Sagitta elegans* shows peculiarities in its distribution in Canadian Atlantic waters. There are at times over 1000 individuals per square metre. Optimum conditions show many of both adults and young, but places occur where only young or only adults are found. This is owing to the peculiar conditions of temperature and salinity. When both young and adults occur at the same place, they are more or less distinctly separated vertically. The adults are found constantly in water of moderate salinity at low temperature; the young in water of low salinity at high temperature. *Eukrohnia hamata* occurs in water of high salinity at low temperature. It is distinctly separated from *S. elegans* vertically, when stratification of the water is most distinct. Currents influence the distribution of both species. *S. elegans* goes to the surface and into shallow water in the colder part of the year and recedes into deeper water as summer warming takes place. Other species show similarly a distribution according to more or less definite conditions of temperature and salinity.

PAPERS OF INTEREST TO ANIMAL ECOLOGISTS

C. Juday, University of Wisconsin. "An Anaerobic Ciliated Protozoan" (10 min.). The hypolimnion of Lake Mendota is devoid of free oxygen from midsummer until early autumn, and a study of the centrifuge plankton of this region during the past three years shows that a free swimming ciliated protozoan occupies a portion or all of this stratum during September and early October. At times as many as 90,000 individuals per litre may be found in certain layers of this water that is devoid of free oxygen. Within two days after the lower water becomes aerated in the autumn this form disappears and is not found again until after the lake has become stratified the following season and the oxygen in the hypolimnion has been greatly reduced or entirely exhausted.

E. B. Powers, Trinity University. "The Minimum Oxygen Requirement of various species of Crayfishes" (15 min.). The value of the crayfish as an index organism as determined by the ability to tide over periods of low oxygen and other adverse conditions. The ability of the crayfish to utilize oxygen at low oxygen pressure as determined by the oxygen content of water at time of death and even without resulting in the death of the crayfish is found to be greatest in *Cambarus immunis* and least in *Cambarus propinquus*, while *C. blandingii acutus* and *C. virilis* are intermediate. The minimum oxygen content of water required for continuous maintenance as determined by a continuous flow of water with low oxygen content is found to be higher than the minimum oxygen content of water in which oxygen can be utilized by the crayfish. In general the respiratory quotient ($\text{CO}_2\text{—O}_2$) of all species of crayfishes tested is higher in low oxygen than in high oxygen content water, thus indicating the ability of the crayfish to tide over a period of low oxygen content.

Minna E. Jewell, University of Illinois. "The Survival of Certain Aquatic Animals in the Absence of Oxygen under different conditions of Acidity and Alkalinity" (15 min.). Certain of the Tubificidae associated with contaminated waters, conditions of low oxygen, and intense putrefaction have been kept alive for two weeks in water acid to rosolic acid under experimental conditions in the complete absence of oxygen detachable by the Winkler method. In water with a higher hydrogen-ion concentration (acid to p. nitrophenol) the duration of life is even longer, while water basic to thymophthalein is rapidly fatal with or without oxygen. Planaria and Chironomid larvae are much less resistant to the absence of oxygen.

A. S. Pearse and **Henrietta Achtenberg**, University of Wisconsin. "The Utilization of the Gases in the Swim Bladder of the Perch" (10 min.). Perch lowered into the stagnant water in Lake Mendota where there was no oxygen lived from one to two hours, while in the stagnated region the oxygen in the swim bladder decreased from about 35 per cent. to 20 per cent.

Albert Hazen Wright, Cornell University. "Fish Succession in the Watercourses of Lake Ontario" (15 min.). Ten streams of Monroe Co., N.Y., were studied in 1904. They are in the bed of Old Lake Iroquois, i.e. postglacial and comparatively recent. Compared with these are streams in the highlands of Ontario, Cayuga Lake tributaries, and a few head-streams of the Susquehanna. Beginning with a diminutive rivulet or developing small creek the first occupants are almost sure to be the common sucker, the horned dace and quite likely the black-nosed dace. The succeeding forms are decidedly soft-rayed species and are more or less in the following sequence: red-bellied minnow; fat-head minnow; red-sided minnow or else Cope's minnow; blunt-nosed minnow; and the common shiner. Then, the diminutive spiny-rayed species and larger carnivores begin to appear, namely: brook stickleback; fan-tailed darter; miller's thumb; river chub; stone-roller minnow; pike, and grass pike. From the beginning of muddy conditions or about the time of the ingress of the pike the successive appearances are: common bullhead; common sunfish; golden shiner; perch; rock bass; large-mouth bass; black bullhead; tadpole cat; mud minnow; Johnny darter; barred killifish; chub sucker; Cayuga minnow; bow-fin; yellow cat; pirate perch; mud darter; and small-mouth bass. The last or so-called swift gravelly group begins with the small-mouth bass followed by the satin-fin minnow; silver-sided minnow; log perch; spot-tail minnow; hog-nosed sucker; silvery minnow; long-nosed dace; eel; lamprey; calico bass; gar; stone cat; green-sided darter; straw-coloured minnow; barred mad tom; red horse; blue-gill; sheepshead and wall-eyed pike. At present the marine two-spined stickleback from the east is entering the Monroe Co. streams while the gizzard shad of the west is invading our Cayuga Lake tributaries.

Alvin R. Cahn, University of Wisconsin. "The Ecology of the Cisco" (10 min.). Many specimens have been taken over a period of two years, at all seasons of the year, and examinations for food, parasites, genital development, age, growth, etc., were made. There is a seasonal migration from the deep water to the shallows in the fall, when the ciscoes spawn, the spawning period lasting about one week and being dependent on the temperature of the water; there is also a nocturnal-diurnal migration up and down, corresponding to a similar movement of the Entomostraca, which form about 95 per cent. of the food of the cisco. Distribution in the lake varies during the year, being dependent on the position of the thermocline.

A. S. Pearse, University of Wisconsin. "The Food of the Shore Fishes of Wisconsin Lakes" (10 min.). An examination was made of 1619 fishes (33 species); the total volumetric percentages of food elements were: insect larvae, 25.2; Entomostraca, 19.1; fish and frogs, 14; adult insects and pupae, 12.3; amphipods and isopods, 12.2; plants, 4.3; mud, silt, and debris, 2.5; Mollusca, 1.9; crayfishes, 1.2.

John N. Lowe, University of Wisconsin. "Food of the Lake Trout" (10 min.). An examination was made of 619 lake trout, 395 of them from Lake Superior and 224 from Lake Michigan. In Lake Superior the food consisted entirely of fish: Longjaw (*Leucichthys zenithicus*), Lawyer (*Lota maculosa*), Miller's Thumbs (*Cottus* sp.). Lake trout in two cases. In Lake Michigan: Cisco of Lake Michigan (*Leucichthys hoyi*), Lawyer (*Lota maculosa*), Miller's Thumbs (*Cottus* sp.), Michigan Lake Herring (*Leucichthys astedi*), Bloater (*Leucichthys* sp.), and lake trout in one case. In all of the 619 stomachs no invertebrate remains were found. The lake trout takes any fish available in the locality in which he happens to be.

John N. Lowe, University of Wisconsin. "Contributions to the Life Histories of the Lake Trout, White Fish, and German Carp, as shown by their scale markings" (10 min.). In all cases the scales examined show annual rings which are an index of the age and rate of growth of the fish.

PAPERS OF INTEREST TO FORESTERS

W. A. Cannon and **E. E. Free**, Desert Laboratory and Johns Hopkins University, respectively. "The Ecological Significance of Soil Aeration" (15 min.). Independent series of experiments have shown that an inhibition of root growth is caused in numerous plants by a decreased amount of oxygen in the soil atmosphere. *Prosopis* maintains growth at very low percentages of oxygen in the soil atmosphere, and a species of *Salix* is able to survive the absence of oxygen. The poor conditions of soil aeration are correlated with the absence of vegetation in the dry lakes of desert basins, and the zonation of vegetation around these basins is possibly in correlation with the different soil aeration requirements of the plants involved.

Carlos G. Bates, Forest Service. "The Rôle of Light in Artificial and Natural Reforestation" (15 min.). An analysis of what is meant by "light," the part which light plays in affecting natural reproduction, and the control of shading of the young planting stock in forest nurseries.

Louis Murphy, introduced by Raphael Zon. "Seeding Habits as a Factor in Competition between Spruce and Balsam Fir" (15 min.). The early fall seed dispersal of red spruce places it at a disadvantage in competition with balsam fir and with hardwoods. At the time spruce seeds ripen and are released conditions in the mixed spruce and fir forests are favourable to immediate germination, followed by winter killing of the new young plants, while balsam seeds fall later and lie over until spring. In the hardwood forest, spruce seed, whether or not it germinates in the fall, is covered with a heavy mantle of hardwood leaf litter. While this mulch is beneficial in the winter, it heats in early spring, under the influence of warm spring rains and direct insolation, before the new foliage is out and in this way stimulates early germination of the spruce seed. This exposes it to the danger of late frosts and damping off.

JOINT SESSION WITH THE BOTANICAL SOCIETY OF AMERICA

John W. Harshberger, University of Pennsylvania. "Convenient Methods in the making of Phytogeographic Maps" (15 min.). The drawing of phytogeographic maps can be facilitated by the use of rubber stamps which represent certain symbols and designate the important plant formations. Each symbol has been especially designed and transferred from a wooden die to a rubber block mounted on a narrow oaken peg.

William S. Cooper, University of Minnesota. "Permanent Quadrats near Alaskan Glaciers" (10 min.). During the summer of 1916 nine permanent quadrats were established in the Glacier Bay region, Alaska, for the study of plant succession after glacial recession.

They were located where the ice edge was known to be at definite dates: in one locality, 1879, in the others, 1899. It will thus be possible to study the progress of the succession from its beginning at a known date. The author hopes to continue the study during future years. The quadrats however are accurately located so that any person visiting the region can find them and record vegetational progress.

Frank C. Gates, Carthage College. "The Revegetation of Taal Volcano, Philippine Islands" (15 min.). Taal Volcano was denuded during the eruption culminating January 30, 1911. Parts of a very few plants in well-protected situations did survive the rain of acid ash and mud. Except for sparing and very local regeneration, no vegetation appeared during the first rainy season, nor to any extent in the dry season following. Revegetation began in earnest in the second rainy season with the invasion of the strand by *Ipomoea pes-caprae* and *Canavalia lineata* and of the lower slopes by the grasses *Saccharum spontaneum*, *S. indicum* and *Themeda gigantea*. Later in the second rainy season, shrubs, *Ficus indica*, *Morinda bracteata* and *Tubernaemontana subglobosa*, and trees, *Acacia jarnesiana* and *Trema amboinensis*, appeared in the grassland. By April 1914 grass was present on the east and west slopes of the crater—the scenes of severest devastation—and a single shrub of *Ficus indica* was growing on a ledge inside the crater some 50 m. below the rim. By March 1915 grass had invaded the floor of the crater. Except where fire had occurred, shrubs and trees were beginning to gain the ascendancy over grass. The temperature of the crater lake diminished through April 1914, but March 1915 found the temperature increasing and bubbling areas in evidence. In March 1915 six species, representing four additional genera and three additional families, were added to the previously recorded flora. The plants found on the island up to March 1915 comprised 9 species of Pteridophytes, 33 of Monocotyledoneae, and 143 of Dicotyledoneae; or 185 species in 147 genera and 60 families.

Frederic E. Clements, University of Minnesota. "Succession in the Petrified Forest Region of Arizona" (15 min.). During the summer of 1916, a study was made of the petrified forests of Arizona from Winslow to Adamana. These represent shale or badland horizons from the Permian Moenocope to the Red Beds of the Triassic and Jurassic. Especial attention was given to the Petrified Forests, the Black, Blue, Red, and Rainbow Forests, in the Adamana National Park. In these the primary xerosere was traced from the pioneer crustose lichens on trunks of *Araucarioxylon* to the final *Bouteloua* climax. The hydrosere is lacking, but is represented in the arroyos by the halosere. Owing to the universal erosion of the shales, the subsere is omnipresent, and furnishes a wealth of detail such as is found only in the most dynamic successional areas.

IMPORTANCE OF FIELD MEETINGS

In a note prefixed to the Society's "Handbook" the late president, Professor Shelford, explains very clearly the importance to ecology of properly designed field meetings in carefully chosen localities. "The development of modern ecology," he says, "has received its greatest impetus in a few localities where there are physiographic conditions giving diversity of habitats in which environmental dynamics are apparent....Many investigators with interest in ecology, and some actually working in the field, have not had an opportunity to see some of the most significant localities in which ecological field study has been conducted, and thus are much handicapped in their understanding of the published accounts, and in relating them to less diagrammatic situations....It is not possible to carry demonstrations of these difficult natural phenomena to the places of meeting of the national societies, as many other materials are carried and displayed as demonstrations. Thus the Society has grown out of an attempt to display the localities which have served to inspire workers in ecological lines."

ON THE VEGETATION OF FOUR DURHAM COAL-MEASURE FELLS.

By HAROLD JEFFREYS.

III. ON WATER-SUPPLY AS AN ECOLOGICAL FACTOR¹.

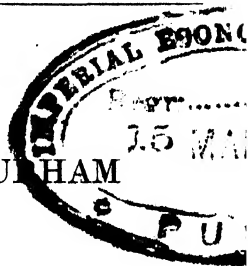
(*With Plate XIX.*)

INTRODUCTION.

It is generally recognised that the supply of water is one of the most fundamental factors governing the distribution of vegetation; yet apart from certain very broad distinctions that have been drawn, few definite results have been obtained about it. In most cases ecologists investigating it have proceeded by methods of correlation alone, which are open to certain objections. Any correlation that is observed between two phenomena is susceptible of two explanations. Either it may be due to a causal connection between the phenomena or it may be accidental. The probability of the latter alternative may be made arbitrarily small by taking a sufficiently large number of observations, but is never actually zero. The former alternative itself is capable of two interpretations. A causal connection may imply that one of the observed phenomena is the cause of the other, but it is also possible that each may react on the other; in this case a part of each must be regarded as caused by the other, so that no sharp distinction between cause and effect is possible. Both phenomena, however, may be caused by something more fundamental than either. The essential point is that correlation is necessarily a symmetrical relation, and as such cannot distinguish between cause and effect. To achieve this object experiment is usually needed.

In the case we are here concerned with, the fundamental factor is the supply of water to the soil either by direct rainfall or by drainage from the higher ground. If this were known completely, and the soil were uniform initially and free from humus, then, other things being equal, at any subsequent time the vegetation would be a function of the position and the time alone. Points with similar water-supply would always have the same vegetation, and the water and humus contents also would be the same, since all the causal conditions are identical. Thus round a saucer-shaped depression or on a uniformly sloping hillside the vegetation should

¹ Parts I and II appeared in this JOURNAL, 4, p. 174.



be similar at the same distance from the base; this is observed to be the case apart from occasional complicating circumstances, the boundaries between associations usually running parallel to the streams.

It may be mentioned that as a mere statement of correlation the last fact is probably more satisfactory than any derived from soil-analyses. For the number of observations that it includes is equal to the number of parts into which the associations can be divided, each being sufficiently large to be considered as showing the essential features of its association; a single statement of this type then really represents thousands of observations, a number which is not approached by even the most careful work by means of analyses, and the probability of its being an accidental result consequent on the use of too few observations is accordingly smaller.

Usually, however, the topography is such that many points with similar water-supply are not at the same level, and in such cases the last statement needs to be qualified. The correlation becomes much more difficult to trace, and complicating phenomena become more important. Experimental treatment then becomes particularly important to establish definitely which of the phenomena observed are due to water-supply.

EXPERIMENTAL WORK ON WATER-SUPPLY.

To trace the effect on the vegetation of variations in water-supply two different methods may be adopted. One may increase the supply at a place where it is low, or diminish it where it is high. The former method requires conspicuous apparatus, and therefore is undesirable where there are many pedestrians. The latter method was used exclusively. The principle adopted was that if a Δ -shaped trench is dug in the ground, the vertex pointing up the slope, the ground inside will receive only the rain that falls directly on it; the surface water from higher ground, which would otherwise form a most important part of its water-supply, is deflected into the trench and drained away without entering the tested area at all. In this way the conditions existing near the base of a slope may be artificially changed so as to resemble those at the top of a hill. If a trench is made in the form of a Y , then above the fork the amount of water reaching the ground is unaltered, but drainage is increased, so that the effective water-supply is reduced. Below the two upper strokes of the Y the surface water does not reach the ground. In the actual experiments it was always found that the effect was greater on the lower side of a trench than on the upper side; this was to be expected.

On April 5th, 1915, four experiments of this type were commenced. On the slope above the South Burn, opposite to the beech plantation, a Δ and a Y were made. The Δ had two straight channels going down the slope, one from each arm, for drainage. Each straight cut in each of these experiments was about 60—70 cms. in length. The breadth was 10 cms.,

and the depth about 15 cms. The vegetation was a dry Nardetum on fine sand, with much *Deschampsia flexuosa*. Two trenches were also made to the north of Alder wood, just on the edge of a Molinietum. The surrounding vegetation was mostly *Nardus*, with *Calluna* and *Deschampsia*. One trench was a Δ like the previous one; the other was of the form Υ . This will henceforth be called the "double Υ ." All were made in such a way that water in the trenches ran out at once instead of remaining in them.

The effect of the reduction in the water-supply was most striking on *Nardus stricta*. The available water in many cases became too scanty for the younger plants. In most cases those that were growing very close to the edge of a trench did not survive through the first summer; some produced a few short leaves, broke off in autumn at the base of the sheaths¹, and did not reappear the next year. In the same way many of those well within the tested areas died at the close of the first or the second summer. The larger plants were affected in a different way. Thus in the double Υ , the heights of a representative set of typical *Nardus* flowering spikes inside in September 1916 were 35, 36, 40, 42, 44, 45, 47, 48, 50 cms.—mean 43.0 ± 3.9 cm. Those in positions outside, at the same distance from the Molinietum and with no hindrance to the run-off, were 47, 48, 50, 50, 52, 54, 55, 55 cms.—mean 51.5 ± 2.1 cms. The reduction in size consequent on the change in the conditions is evident.

Similarly the lengths of typical leaves inside were 19, 20, 23, 23, 26 cms.—mean 22.2 ± 2.1 cms.; and outside 20, 23, 27, 27, 28, 28, 29 cms.—mean 26.0 ± 2.8 cms. In 1915 there was only one flower-spike of *Nardus* within this area. In examining the leaves it was necessary to take an equal proportion of upper and lower leaves, as the lower tend to be the shortest.

In the Δ close by, in September, 1915, the lengths of *Nardus* leaves measured were

12, 15, 16, 18, 21 cms. Mean 16.4 ± 2.2 cms.,

and outside 17, 17, 18, 19, 19, 22, 28 cms. Mean 20.0 ± 2.6 cms.

In September, 1916, the leaves inside gave

17, 18, 19, 20, 21, 23 cms. Mean 19.7 ± 1.4 cms.

and outside 21, 23, 23, 24, 24, 24, 26, 27, 28 cms. Mean 24.4 ± 1.4 cms.; the flower spikes inside gave

37, 39, 39, 40, 42, 45 cms. Mean 40.3 ± 1.7 cms.,

and outside 53, 55, 57, 58, 58, 59, 59, 60 cms. Mean 57.4 ± 1.3 cms.

Similar results were obtained in the other experiments. Thus the reduction in the water-supply caused a large reduction in the tissue of the *Nardus*. Very large *Nardus* clumps in some of the experimental areas were found in 1916 to have lost a great deal of the ground they formerly occupied, purely on account of the shortening of the lower leaves, which had formerly covered it. Such clumps in the ordinary course of events would probably have

¹ See p. 133.

grown considerably in the time. Instead of this their effective size diminished, and some of them actually lost some of their outlying branches, so that the true size also became smaller. Ground set free by *Nardus* in any of these ways was usually seized by *Deschampsia flexuosa*, with which a large quantity of *Festuca ovina* was associated.

In the double **Y**, most of the area between the two straight cuts on the left was covered with *Nardus* initially. Scattered about between the tussocks however were a few small seedlings of *Calluna*, evidently in their first year, and almost covered with a dense mass of *Nardus* leaves. In September, 1915, some ground had been left vacant on one side owing to the reduction of the size of the *Nardus*; on this a few seedlings of *Calluna* were growing, but in June of the next year the whole of this bare area was covered with a dense growth of young *Calluna* plants, the seedlings having at the same time increased very much in size; at the sides the *Calluna* was spreading over the *Nardus* in September. At the same time the seedlings in the middle of the *Nardus* had grown to such an extent as to be spreading their branches over the top of it, thus occupying a considerable area. In August they flowered profusely. It may be regarded as almost certain that in a few years the *Nardus* will be quite overwhelmed by *Calluna*; for it has been shown (see p. 145) that the shade of *Pteris* fronds is enough to destroy *Nardus*, and *Calluna* casts a much deeper shade than *Pteris*. At the same time in the upper part of the same area *Calluna* spread a great deal at the expense of *Deschampsia*.

A feature of all these experiments was the large increase that resulted in the quantity of *Potentilla erecta*. Initially a few plants of *Juncus effusus* grew near the lower fork of the double **Y**; during the first summer only one of them produced flowers, which were very few in number. The next year the other plants were all dead, and the survivor only produced a cluster of three flowers. The vacated area was reoccupied by *Deschampsia*.

The effect on *Molinia* was similar to that on *Nardus*, although on account of the small number of tussocks within the areas tested it was not so important. Several *Molinia* clumps of small size however disappeared during the experiment, being replaced by *Deschampsia*. In September, 1915, the heights of spikes of *Molinia* in the **A** beside the alder wood were 23, 27, 29, 32, 36, 38, 39, 43, 43, 45 cms. In parts outside the area, equally distant from the main *Molinia* mass at the bottom, the heights ranged from 45 to 64 cms. In 1916 similarly the heights inside ranged from 34 to 45 cms., and outside from 60 to 67 cms. The lengths of leaves inside were 10, 15, and 16 cms., and outside 14, 16, 17, 18, 20, 21, 22 cms. The numbers of upper and lower leaves respectively were in about the same ratio in both cases.

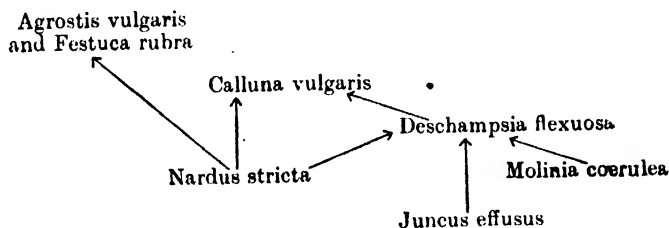
Deschampsia flexuosa appeared to be affected very little. In the **A** opposite the beech wood the average height of its flowering spikes was 43 cms., while that of the spikes outside was 42 cms. The alteration was so small

that it appeared as if the water-supply was not very different from the optimum for *Deschampsia*. At the same time the tallest *Nardus* spike in the area was 28 cms. high, while those outside ranged from 35—39 cms.

In addition to the experimental trenches, which were made for the purpose, much information has been obtained from other trenches that have been made on Waldrige and Birtley Fells. Thus, at Waldrige a ditch $\frac{1}{2}$ metre wide and $\frac{1}{2}$ metre deep was made in 1914 through a *Nardetum* on clay near the Edmondsley road. The refuse was placed on the south side, and in 1915 was dominated by *Agrostis vulgaris* and *Festuca rubra*. On the north side the *Nardus* was very stunted in 1915. There was no *Deschampsia* near; *Agrostis* and *Festuca* came right up to the edge of the trench. The next year *Nardus* was still more stunted, its leaves being only 8 cms. long in the driest parts, and it did not flower. There is little doubt that if the drainage continues this *Nardetum* will change completely to dry grassland in a few years, as indeed it has almost done now. Along similar trenches on Birtley Fell, *Nardus* was replaced by *Agrostis vulgaris* and *Festuca ovina*. The succession in many cases was complete in a year.

In the bottom of these trenches the increased water-supply produced some striking effects. Where no water was standing, *Agrostis vulgaris* was 50 cms. high, and *Festuca ovina* 25 cms. Where it was standing in local depressions, *A. alba* was growing to a height of 40 cms. It could be distinguished at once from the wet form of *A. vulgaris* by its much more slender habit. In the ditch at Waldrige just described, *A. vulgaris* was dominant, with *Holcus lanatus*, *Anthoxanthum*, and *Trifolium repens* abundant¹.

Successions due to reduction of water-supply.



THE VEGETATIVE PROPERTIES OF *NARDUS*.

Nardus stricta is a perennial. It spreads by means of a rhizome about 2 mm. thick, from which rises a closely packed series of bundles of leaf sheaths, two or three abreast. In one year the rhizome only grows about 20 mm., and the next year it continues to extend

¹ In charting these experimental areas in the open the writer has found a folding drawing-board exceedingly useful. It is made of mahogany, in two pieces each 22 × 11 × 1.5 cms., hinged together by their long sides. It can be carried easily in an ordinary vasculum, leaving space for a trowel and measuring tape; when open a piece of unfolded note-paper is pinned on it on the side opposite to the hinges. If necessary a strut could be inserted to prevent the board from folding backwards while in use, but in practice the stiffness of the hinges has been found enough to make this unnecessary.

in the same manner in the same direction. All the lower leaves spread out nearly horizontally, and cover a semicircle, none pointing towards the old part of the rhizome. This old rhizome, with the roots and sheaths attached to it, persists for several years, but ceases to have any vegetative function. The rhizome may branch. When it does, the branching is usually dichotomous. The groups of bundles have corresponding groups of cord roots, but the number of roots per bundle may range from 1 to 5. At the sides of each bundle are sheaths 10 mm. long and 3 mm. broad, considerably broader than the true leaf sheaths. The bases of the sheaths are swollen, so that the whole bundle (containing about three sheaths) is about 4-5 mm. thick, and exceedingly hard. The roots are long, thick, and very tough. The sheaths rise vertically for 15 mm., and then the leaves suddenly spread out at right angles. The upper leaves grow out in all directions, so that the whole clump is almost hemispherical, and when full grown, of about 15 cms. radius in suitable circumstances.

In the autumn the leaves and sheaths dry and become bleached. This occurs soonest in the driest parts of the Nardetum, which consequently is extremely conspicuous in autumn and winter. It becomes green again about May, when the young leaves commence to grow. The roots are liable to break near the top just after drying, and thus large numbers of whole tufts may be found scattered about loose during the winter.

THE LOWER MARGIN OF THE NARDETUM.

Where a Nardetum surrounds a *Juncus effusus* bog, the boundary between the two associations is nearly always remarkably horizontal. There is no conspicuous reason in summer for the extreme closeness of the approximation that is found, but in winter it is seen that the boundary is just at the level to which the ground is submerged in surface-water, which stays there till the spring. Above the margin the association is usually a wet Nardetum, while below it *Juncus effusus* occurs, with *Carex goodenowii* or *Agrostis alba* and no *Nardus* whatever. *Molinia* also is observed to occur rarely except where the water level in winter is somewhat above the surface. It was thought especially desirable to verify experimentally whether the conditions in winter were thus capable of determining the ability of *Nardus* to grow in certain places, as hitherto in questions of demarcation of associations by soil-humidity the summer conditions alone have usually been considered. For this purpose four *Nardus* clumps, each about 10 cms. across, were taken from Birtley Fell on October 1st, 1915. Their normal soil was taken with them. It contained much *Calluna* bark at a depth of 3 to 4 cms., and below this a rather hard purplish pan of sand, several inches deep. No *Calluna* was growing near at the time though it was formerly present. *Agrostis vulgaris*, *Triodia decumbens*, *Luzula multiflora* and *Potentilla erecta* were associated with the *Nardus*. These clumps were planted in clay flower-pots, and placed in a tin plated vessel of water, in such a way that one was submerged to the base of the uppermost leaves, another to just below the surface of the soil, and the other two so that depths of about 5 and 8 cms. respectively of the soil were out of the water. As far as possible the level of the water was kept constant throughout the winter. In April the plants were just commencing to grow.

The same conditions being continued, it was found at the end of June that the submerged *Nardus* clump was dead, except the central shoot, which had produced a single leaf-bundle and one flower-spike. The others were all flowering profusely. The associated plants all flowered, save the tormentil in the submerged one, which has not reappeared. From the beginning of July to the middle of October the level of the water was kept about 10 cms. lower, so as to make the conditions correspond more nearly with the natural summer conditions. In September the lowest plant of *Nardus* had made little progress; only one flower spike had been produced, and the whole plant was almost smothered by a dense growth of *Agrostis vulgaris* and *Luzula multiflora*. The other *Nardus* plants were in full fruit, and the associated plants were confined to the edges of the pots, to which the *Nardus* had not spread.

Evidently then submersion in winter has an exceedingly injurious effect on *Nardus*, which is barely able to survive after a single winter of it, and cannot after it prevent itself from being covered by such a plant as *Agrostis vulgaris*, which is not a normal inhabitant of areas that are ever submerged. It has not been ascertained as yet whether it can survive a second winter at all, but in any case its growth is so feeble that it is certain to be defeated by *Juncus* spp. or *Molinia*, which normally are dominant and grow strongly on the same type of ground¹.

THE REPRODUCTION OF *PTERIS* BY SPORES.

It is well known that the spores of any fern require a considerable amount of moisture before they can germinate. This is a matter of extreme importance in the ecology of *Pteris aquilina*, for it has already been remarked that it tends to grow principally on elevated and dry ground and stops abruptly where the drainage is bad. In consequence of this the type of area such as dry grassland, Deschampsietum, or dry Nardetum, in which *Pteris* tends to spread most rapidly by rhizomes, is unsuited for its propagation by spores. If however there is a local area within one of these associations in which there is sufficient moisture for the spores to germinate, then windblown spores may cause a few isolated fronds to spring up there, and bracken will spread from these by means of its rhizomes. The influence of a disused rabbit hole in this direction has already been commented upon by E. P. Farrow².

In the disused Smithydene quarries, the slope up to the Fell is very dry boulder-clay, with *Deschampsia flexuosa* and *Festuca ovina*. Where there is a slight local excess of moisture *Nardus* may occur. In cracks in the clay

¹ An analogous case is that of the cotton plant, described by W. L. Balls, *The Cotton Plant in Egypt*, p. 38. When the water table reaches its roots, all those roots below the surface are in a few weeks not only dead but decomposed. This is attributed to asphyxiation.

² This JOURNAL, 8, 1915, Plate XX, photos 7 and 8.

near the top, a few small bracken plants grow. They are twenty metres from the nearest bracken area, and it is probable that the cracks have held sufficient moisture for spores to be able to germinate, thus acting in an analogous way to the rabbit hole. In the bed of Stream 8, which is usually dry, *Pteris* occurs in small quantities among the *Juncus effusus*. If it were a permanent stream, bracken certainly could not grow there. It is possible that the occasional flushing gives the rush all the moisture it needs without destroying the bracken, which must have been initially spore-sown, as there is a wet Nardetum with no bracken between the stream and the nearest *Pteris* area.

It has been stated already that under bushes, such as *Ulex* and *Calluna*, the water content is greater than at surrounding points, on account of the reduction of evaporation. This accounts for several striking occurrences. The water-supply necessary for *Calluna* is less than that required by *Nardus*; yet on account of the much greater induced water-content¹, the total water-content below *Calluna*, even in a well-developed Callunetum, is usually greater than that in a Nardetum. In consequence very moisture-loving plants may be found among *Ulex* and *Calluna* where there is room. Thus, *Juncus effusus* is frequently seen rising up through an isolated *Calluna* bush, although it may be absent from the surrounding Nardetum. The only locality for *Ophioglossum vulgatum* at Walldridge is under a *Ulex* bush. In accordance with these facts, it appears that the ground below these shrubs also affords a suitable amount of moisture for the germination of bracken spores. This is probably the reason for the concentration of *Pteris* in the Callunetum, mentioned in the second part of this paper². Further, a single plant of bracken may often be seen, quite isolated from all others, in the midst of a *Ulex* or *Calluna* bush. This is a matter of extreme importance; such a plant may serve as a base for rhizome growth, thus commencing a new Pteridetum, and in case the bush dies or is burnt, *Pteris* is already on the spot, and becomes dominant before the bush has time to regenerate³. It may be mentioned here that the only plants of *Pteris* on the main part of Birtley Fell are a few sporelings growing in *Ulex* bushes.

GENERAL OBSERVATIONS ON WATER-SUPPLY.

From the experimental results it is evident that the zonation *Calluna-Deschampsia-Nardus* can be produced by increasing water-supply, and also that the Nardetum by diminution of water-supply can be changed to dry grassland. Now the dry grassland occurs on the very driest places, such as on steep shale heaps and on certain especially dry sunny slopes; the last includes that at Tinkler Fell. These places are probably too dry for *Calluna*, and while it is certain that the dry grassland must come before *Nardus* in the above zonation, it is highly probable that it should come

¹ See later, p. 138.

² This JOURNAL, 4, p. 184.

³ See later, p. 141.

before *Calluna*. This was confirmed by an observation on Muggleswick Common, in the north-west of Durham, where a *Callunetum* on sand with a surface layer of peaty humus contained much *Agrostis vulgaris*. Sods were cut from this and allowed to dry in the open. The roots of the *Calluna* were shallow, and did not reach the bottom of these sods. In most cases the *Calluna* was dead, but *Agrostis* and *Festuca ovina* still survived and were increasing. The *Calluna* that survived had not flowered, and was evidently receding.

On ground with a greater water-supply than the wet *Nardetum* other associations occur, but the determining factor is the level of the ground water in winter; the conditions in summer do not affect the lower limit of the *Nardetum*. A distinction may then be drawn between the associations that are on ground submerged in winter and those that are not. Thus the zonation *Agrostis*-*Calluna*-*Deschampsia*-*Nardus*, in which *Calluna* and *Deschampsia* may be replaced by *Pteris* or *Holcus mollis*, and *Calluna* and *Nardus* partly replaced by *Ulex*, constitutes the vegetation of ground that is not submerged in winter; *Agrostis alba*, *Molinia*, *Juncus* spp. and *Carex goodenowii* dominate ground that is submerged in winter but not in summer. The factors that separate them are doubtful. *Agrostis alba* usually occurs where there is a plentiful but intermittent supply of fresh water, and the surface is dry for a considerable part of the summer. *Molinia*¹ and *Carex goodenowii* usually grow where there is a large amount of humus in the soil and the water-supply is peaty in character. The various *Junceta* receive more water in winter, and *Juncus effusus* generally occurs where the drainage is bad.

The presence of much organic matter in the soil and the surface water may be the reason why *Molinia* occasionally occurs instead of *Nardus* where the ground is not submerged in winter. In the spring of 1916 many sods were cut on Birtley Fell in an area containing both these plants, and allowed to lie in the open. The effect of the exposure was that in June *Nardus* was dead. *Molinia* was scarcely affected; *Agrostis vulgaris*, *Festuca ovina*, *Calluna*, *Luzula campestris*, *Potentilla erecta*, and *Galium saxatile* were flourishing. From this it would appear to be very dangerous to assume that a great general water-supply in summer (rather than in winter) would favour *Molinia* at the expense of *Nardus*. The organic matter and dissolved substances are likely to be of greater importance.

¹ This statement does not I think contradict that of Rev. T. A. Jeffries, "Ecology of the Purple Heath Grass (*Molinia coerulæ*)," this JOURNAL, June, 1915. He states that *Molinia* grows where the ground is frequently flushed with rain water, but as the rain water must contain peaty substances from the Eriophoreta its composition is probably not much different from that at Waldrige. If this interpretation be correct *Molinia* may be regarded as intermediate between *Agrostis alba* and *Eriophorum vaginatum*.

RESULTS OF ANALYSES OF SOILS.

While water-supply is the master factor in determining the distribution of vegetation in the areas described in this paper, a difficulty arises when one wishes to compare the distributions in different localities. It is simple in a single locality to trace the zonations depending on it, for the boundaries usually run very nearly parallel to the base of a slope. If however the same zonation occurs elsewhere, it becomes desirable to compare the two localities quantitatively; to do this directly is however difficult on account of differences in rainfall, slope, and soil-composition which must be allowed for. The natural procedure would be to attempt to find some criterion based directly on the composition of the soil itself and the percentage of water contained. There are however both theoretical and observational objections to the use of the percentage of water in the soil as a criterion of water-supply. In the first place, it is necessary to take the sample at a single definite time, that usually chosen being during the growing season and not immediately after rain. The former restriction now seems incorrect, in view of the great importance of the conditions in winter in determining the distribution of *Nardus*; the second restriction also appears arbitrary, for occasional flushing has a considerable effect on the distribution of certain plants, such as *Molinia*, and would not be recorded in the analysis of a sample not taken immediately after rain. In the second place, although the water-supply is one of the fundamental causes of vegetation, and is not itself changed by it, yet the growth of plants reacts on the composition of the soil in several ways, the most obvious of which are as follows:

- (1) the humus content is increased by the decay of vegetable matter;
- (2) evaporation is diminished to a considerable extent, which seems to become greater the taller the dominant plant¹;
- (3) large quantities of surface water remain absorbed by the humus instead of being drained away;
- (4) water is used up to satisfy the physiological requirements of the plants.

The importance of these effects cannot be expected to be the same for all plants; thus the water-content at any instant, in addition to the part caused *directly* by the water-supply, also contains a part that must be regarded as caused by the vegetation and only *indirectly* by the water-supply. This will be referred to as the *induced* water-content. Similarly there is an induced humus-content. Now while (with the same composition of the mineral part of the soil) the water-supply determines the vegetation uniquely for any value of the time, so that the *total* water-content is fixed when the water-supply is fixed, the converse is not necessarily true. For the plant that

¹ F. E. Fritsch and E. J. Salisbury, "Further Observations on the heath associations on Hindhead Common," *New Phytologist*, 14, 1915, p. 123.

grows where the water-supply is small may have a greater inducing effect than one that grows where the supply is greater, and if this is the case the area with the larger water-supply may actually have the smaller water-content. Thus while water-content is a single valued function of the water-supply, we cannot assume the converse to be true without a great deal of evidence. It has actually been shown by Crump¹ that the vegetation is not determined when the water-content is known. He suggested in its place the "coefficient of humidity," defined as the ratio of water-content to humus-content. Briggs and McLane² have suggested the ratio $\text{Water} \div (.57 \text{ humus} + .57 \text{ clay} + .12 \text{ silt} + .03 \text{ sand})$. Until it can be shown, however, that either of these numbers is free from any part induced by the vegetation, it will be impossible to regard a knowledge of one of them as determining either the water-supply or the vegetation. Nevertheless as items in the description of associations the soil analyses may be valuable. The samples described later were taken from various parts of Walldridge Fell, in September, 1915, not after rain, by boring 10 cms. deep, this being the level of the greater portion of the roots of the respective dominants.

The method of analysis employed was as follows:

The sample was reduced to as nearly homogeneous a condition as possible without the use of a pestle, roots having been removed. A portion was then weighed out into a porcelain crucible, and this was heated in a steam oven till no further loss of weight took place. The total loss gave the water. The dried soil was then ignited till no further loss took place, the loss being recorded as humus. The residue was mixed with slightly ammoniacal water, covered to a depth of 7.5 cms., and allowed to stand for $12\frac{1}{2}$ minutes. The supernatant liquor was poured off and the process repeated till there was no suspended matter on standing for $12\frac{1}{2}$ minutes. The suspended matter in the supernatant liquor was recorded as "clay and fine silt" and the residue as "sand and gravel." Almost the whole of the suspended matter settled in 24 hours, so that the true clay was small in amount.

The acidity was determined subsequently by washing a weighed sample of the soil till the washings were neutral, and titrating the filtrate with N/500 caustic soda and phenol-phthalein. It is expressed in c.c. of decinormal acid per 100 grms. of soil.

Soil Analyses.

	Callunetum	Deschamps- ietum	Dry Nardetum	Wet Nardetum	Molinietum	Caricetum goodenowii
Water ...	60.7	19.3	22.9	49.3	77.1	78.5
Humus ...	25.3	5.8	12.1	5.3	12.2	8.4
Fine silt ...	4.0	0.8	13.2	6.0	4.1	5.8
Sand ...	10.0	71.1	51.8	44.4	6.0	7.3
Acid ...	4.94	1.80	3.42	1.42	2.86	0.92
Water/humus ...	2.4	3.3	1.9	9.3	6.3	9.3

¹ W. B. Crump, *New Phytologist*, **12**, 1913, pp. 125-147.

² U.S. Dept of Agriculture, Bureau of Soils, *Bulletin* **45**, 1907.

			Pteridetum (Hill 2)	Holcetum mollis (Hill 13)
Water	17.0	21.4
Humus	7.0	6.7
Fine silt	8.4	0.8
Sand	67.6	71.1
Acid	1.60	1.80
Water/humus	2.4	3.2

Zonation round Bog 1.

			Pteridetum	Dry Nardetum	Wet Nardetum	Juncetum effusi
Water	43.6	45.8	62.8	41.4
Humus	10.3	13.1	12.3	9.5
Fine silt	0.7	5.2	6.5	16.5
Sand	45.4	35.9	18.4	32.6
Acid	1.94	1.66	1.76	1.80
Water/humus	4.2	3.5	5.1	4.4

A striking example of the effect of induced water-content may be seen in the above Callunetum. Although *Calluna* requires a smaller water-supply than *Nardus*, the water-content below it is greater than in three of the Nardeta examined, and only slightly less than the wettest. This is probably due partly to restriction of evaporation and partly to the power of retaining moisture possessed by the humus. Similarly in the last zonation, the *Juncus effusus* bog in dry weather actually has the smallest water-content of the series, probably owing to the ready evaporation from the exposed ground between the plants. As a criterion for determining zonations due to water-supply, then, water-content is clearly unsatisfactory. The ratio of water to humus is very little better. In the zonation round Bog 1 it shows no consistent progression, while different Nardeta show both the highest and lowest coefficients of humidity in the whole series. Making a correction for sand and silt does not improve matters. None of the criteria yet offered is satisfactory in the sense that it steadily changes in the same direction as we pass through any zonation, and until one is found that will represent a single zonation properly, it is clearly useless to hope to find one that will represent them all.

IV. ON VARIOUS OTHER ECOLOGICAL FACTORS.

THE EFFECTS OF BURNING.

Fire is among the most important ecological factors on three of the four heaths here described. On Tinkler Fell burning is done periodically and systematically, the purpose being to encourage the production of young shoots of *Calluna*, which are a favourite food of grouse. At Waldrige and Birtley heath fires are frequent, but rarely extensive. They seldom reach more than a few yards from their starting points. Some are accidental, but the majority are started by the inhabitants purely for amusement. These fires

are probably the most important cause of the succession from *Ulex* and *Calluna* to *Pteris*, on account of their selective effect on shrubs.

Such a selective effect may obviously be expected to occur. For when a shrub is burnt to the ground, it cannot become dominant again for several years, on account of its slowness of growth. Grasses and certain other plants, however, can colonise the vacant area at once by wind-blown seeds or vegetative growth, thus attaining temporary dominance, which may become permanent if they can succeed in overwhelming the seedlings or young shoots of the shrub. If they do not so succeed, the shrub will regenerate, as indeed it usually does. Every bush, however, that is destroyed in this way represents a certain loss of territory to its association, though the loss may be only temporary.

An agency that may mitigate the effect is the formation of a layer of charred refuse where the bush was. This appears to be somewhat difficult to colonise. The roots of herbs, also, are frequently destroyed, whereas those of the shrub in many cases are not. The first plants to become established on a burnt area are thus necessarily of a somewhat select character.

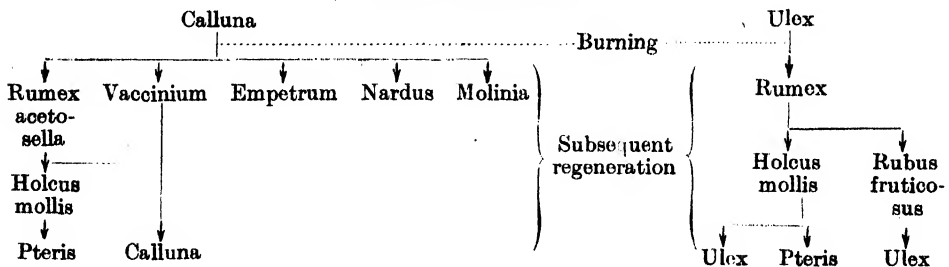
When *Ulex* bushes are burnt, the first colonist seems to be always *Rumex acetosella*, which generally appears in the first year after the fire. *Holcus mollis* comes later, and spreads so rapidly that it becomes dominant over the burnt area in about the third year. This stage, however, is only transient. *Holcus* is unable to prevent the regeneration of the *Ulex*, and about twelve years after a fire a new bush is generally to be found, with an undergrowth of *Holcus mollis*. If the fire occurs in the spring, new shoots may be sent up from the old roots in the autumn of the same year, but in the majority of cases the *Ulex* waits till the next year before sprouting again. Often the roots are killed, and then recolonisation by seeds is necessary. Bilberry, *Galium saxatile*, Bramble, *Potentilla erecta*, and *Agrostis vulgaris* are all capable of colonising a burnt *Ulex* area, although they are not nearly so constant as the two plants mentioned above. *Deschampsia flexuosa* and *Festuca ovina* rarely occur, and apparently *Nardus* never does, even when it surrounds the area.

On the part of Tinkler Fell to the north of the road, the succession when *Calluna* is burnt is to *Rumex acetosella*, then to *Holcus mollis*, and finally to *Calluna* again. At Walldridge, however, the succession is altogether different. *Holcus* and *Rumex* do not usually appear, but *Nardus*, *Vaccinium myrtillus* and *Empetrum nigrum* all spring away much more rapidly than *Calluna* does. This seems to be the usual cause of local patches within the Callunetum that are monopolised by *Vaccinium* and *Empetrum*. *Deschampsia flexuosa* also springs up quite early. *Spergularia rubra* has been known to appear. At Birtley the succession usually resembles that on Tinkler Fell, but sometimes *Vaccinium* or *Molinia* may appear; the latter occurs in the damper parts of the Callunetum.

The whole succession is altered if bracken succeeds in establishing itself before the regeneration of the shrub is complete. It has not been shown to be capable of doing this in the ordinary case where a bush has been burnt at a considerable distance from the nearest bracken area, presumably because the ground is too dry for the spores to be able to germinate. On the other hand, if it invades the burnt patch by rhizome growth from a neighbouring *Pteridetum*, or if a few individuals of it were growing among the shrub before burning took place, then the fire removes the competition of the shrub, and the bracken is free to propagate itself vegetatively without hindrance. It has several times been stated already¹ that bracken tends to reappear in larger quantities after burning, and this phenomenon has repeatedly been observed at Waldrige. In quite a short time, often as early as the second year, it assumes local dominance; *Holcus mollis* or *Vaccinium*, as the case may be, is subdominant. The original shrub appears never to regenerate in these circumstances, being quite unable to grow under the bracken. There is a whole hillside at Waldrige which was formerly a *Ulicetum*, the charred remains of which can still be traced; it is now covered with bracken, *Holcus mollis* being sub-dominant. The upper edge is now marked by scattered *Ulex* bushes, all that are left of the original association.

Rubus fruticosus behaves very similarly to *Pteris* after a fire, but as it does not spread so rapidly its importance is not nearly so great. Further, it cannot prevent the regeneration of the shrub.

Burn Successions.



THE INFLUENCE OF BRACKEN ON ITS COMPETITORS.

The scantiness of the vegetation associated with *Pteris aquilina* has already been noticed. Where bracken has invaded a former *Calluna* or *Ulex* association, in many cases no trace of the original community is left, except perhaps some characteristic refuse that may be left in the humus. When it becomes completely dominant, in nearly all cases there is no associated vascular vegetation whatever except, in special cases, *Holcus mollis*. In more open areas, *Deschampsia flexuosa*, *Calluna*, and *Vaccinium* occur, but even these disappear in the densest places. The most obvious

¹ F. E. Fritsch and W. M. Parker, *New Phytologist*, 12, 1913, p. 148. Elgee, Frank, this JOURNAL, 1, 1913, p. 12.

explanation of the lack of associated vegetation is that the bracken prevents any plants below it from receiving a sufficient quantity of light to enable them to hold their own. To test this hypothesis a series of determinations of the light-intensities below *Pteris* and below various other plants was made by means of an Imperial photographic exposure meter and a stop-watch. The intensity of the light is given by the time it takes a piece of photographic paper of a definite sensitiveness to darken to a standard tint. There was some variation in the colour of the light below different plants, but as the prevailing colour of the surroundings in all cases was green, this variation was probably insufficient to make much difference. It was found that at no place in the bracken association is the light intensity less than $\frac{1}{20}$ of what it is in the open; whereas *Vaccinium* and *Deschampsia* were growing well under *Calluna*, with a light ratio of $\frac{1}{100}$, and *Deschampsia* and *Holcus mollis* were found under *Ulex*, with a ratio of $\frac{1}{30}$. It is evident, then, that the cutting off of the light by bracken is not by itself sufficient to account for the absence of these three plants below it where it is growing most luxuriantly. *Calluna*, on the other hand, never seems to exist where the ratio is less than $\frac{1}{10}$ (it has only once been found where it was less than $\frac{1}{3}$) and *Nardus* ceases to grow where it is less than $\frac{1}{3}$. It therefore seemed possible that light might be the factor that limits these two plants.

A further phenomenon was noticed, however. It was repeatedly observed that under bracken, where the dead fronds of the previous year were lying, *Deschampsia* was either absent or very scanty, even though a few inches away, with the same light intensity, it was subdominant in the absence of bracken refuse. Where many dead fronds lay, no vegetation of any kind occurred. This correlation was complete. *Holcus mollis* appeared to grow under a larger quantity of refuse than any other plant, but the observations were insufficient in number to establish this satisfactorily. A similar phenomenon was observed where pine needles of the previous year were lying on the ground in plantations.

A series of experiments was next made to ascertain if possible the reason for these observed correlations. It was found that under such a layer of bracken refuse as actually occurs in nature, the light ratio is often as small as $\frac{1}{40}$, so that the reduction of intensity is much greater than is caused by the living bracken alone. This further reduction then gave one possible cause; another was the restriction of evaporation by the refuse, which acts as a mulch and thus increases the water content of the soil. A third was that there might be in the bracken fronds and pine needles some substance which when the tissues decomposed would give rise to a poison that would destroy other vegetation. If any of these suggestions were correct, then when a layer of fresh bracken fronds, equal in depth to what occurs on the heaths, is spread on an area covered with vegetation, that vegetation should be killed when decomposition is complete. If the death took place after

the commencement of decomposition, the third alternative would be expected to be correct; further, if bracken were dug in beneath the roots of other plants, and these died in consequence, the third would be correct. On the other hand, if death took place before the commencement of decomposition, the first or second alternative would be chosen, unless a toxin was washed out of the newly fallen frond by rain. This however does not appear to occur. In this case the death should take place at the same time when an equivalent quantity of some inert substance is placed on the herbage. A set of experiments to test these points was commenced in September, 1915, on various parts of Walldridge and Beamish Fells.

Near Stream 8 a burnt gorse patch was found with many seedlings in their first year, still bearing the cotyledons, growing on it. Over half of it bracken fronds were laid about three deep, this being the number most commonly occurring in areas covered by that plant. In April, 1916, all those seedlings that had been covered in this way were etiolated and dead. They still bore their cotyledons, and appeared to have grown no more after the bracken was placed upon them. Those growing round about, where there was no bracken or only a single layer of it, were quite healthy and are still growing in the normal way. Evidently then the effect of bracken fronds when undecomposed is capable of destroying *Ulex* seedlings; the dense growth of *Pteris* that appears after the burning of a *Ulex* bush can thus prevent the regeneration of the *Ulex* from seed. It has been already remarked that *Ulex* can grow in exceedingly damp ground, so that the increase in the water content is not likely to be the reason for the effect; it is most probable, then, that the cutting off of light is at any rate a sufficient reason for the defeat of *Ulex* by *Pteris*.

On Beamish Fell three experiments were made to test the effect of *Pteris* on *Deschampsia flexuosa*. In the first, the grass was covered with a layer of pine shavings estimated to be about equivalent in power of stopping light to three layers of bracken. These were chosen as the most inert substance that was easily accessible and likely to remain in the same place for a year. In the course of the experiment they actually behaved as inert. In the second, bracken fronds were placed on the grass; and in the third, the turf was lifted to a depth greater than that of the roots, and bracken dug into the subsoil. Care was taken not to injure the roots. In the next April the bracken dug into the earth was decomposed and the grass growing above it was dead, showing that the toxic effect of the fronds was enough to destroy *Deschampsia*. At the same time the bracken on the surface was not decomposed, and the only visible effect was that the grass, owing to increased moisture, was greener than elsewhere and had commenced its vernal growth earlier. The effect of the pine shavings was similar. In July little further change had taken place. In September, 1916, the decomposition had advanced considerably, and most of the *Deschampsia* below the fronds was

dead. Pine refuse placed either above or below *Deschampsia* produced a similar destructive effect. When it was placed below, the decomposition was complete in July, but when above it was only partial¹. In many other parts of Beamish Fell it was observed in April, 1916, that where bracken was decomposing *Deschampsia* below it was dead. A comparatively thin layer was enough: a single frond decomposed left a line of dead *Deschampsia* along its whole length. Four undecomposed fronds were not enough to destroy the same plant. Where *Deschampsia* and *Holcus mollis* were growing side by side, with bracken rotting on them, practically all of the former was dead except one small terminal tuft, whereas *Holcus mollis* was growing quite strongly up through a heap of refuse. Similar experiments at Waldrige led to similar results. It is evident then that the principal reason why bracken defeats *Deschampsia flexuosa* is the toxic effect of the decomposing fronds; bracken has no important effect on *Holcus mollis*.

At Waldrige, in a mixed association above the Alder wood, a further set of experiments was made. Bracken was laid on *Calluna*, *Nardus*, and *Vaccinium myrtillus*, and also dug in below the two former. The *Calluna* with bracken under it was dead in December, and the *Nardus* in April. Where bracken was placed on the top of *Calluna* and *Nardus*, both were killed in April. Decomposition was already far advanced. The experiment on *Vaccinium* was unfortunately spoilt by a fire before it was complete. Several experiments on *Calluna* were made, and all gave the same result; so that while no definite evidence was obtained to show whether shade has an important effect on *Calluna*, it was shown that the toxic effect of the decomposing fronds was sufficient to destroy it. In the case of *Nardus*, the effect was the same whether the fronds had decomposed or not, this being shown by a further experiment carried out in the summer of 1916. Thus the shade effect and the toxic effect are each separately sufficient to destroy *Nardus*.

The principal reason, then, why there is no other vegetation under a dense growth of bracken is that its competitors are unable to grow among the refuse left by the bracken. Whether they fail to grow there on account of the extra shade of the dead leaves or on account of a toxic effect of the decomposing tissues depends on the particular competitor that is being considered, thus:

Ulex is destroyed by the cutting off of light.

Calluna is killed by the toxic effect. The effect of shade is undetermined².

Nardus stricta is killed by either the shade effect or the toxic effect separately.

¹ Cf. E. P. Farrow, "On the Ecology of the Vegetation of Breckland," this JOURNAL, 5, "V. Observations relating to competition between plants," p. 172 (present issue). No mat was formed in the present case.

² E. P. Farrow, loc. cit. p. 165, considers the effect of shade to be sufficient, as *Calluna* can be killed by either factor separately.

Deschampsia flexuosa is killed by the toxic effect, but not by the shade.

Holcus mollis is not much affected by either factor¹.

ON THE RATES OF SPREAD OF VARIOUS PLANTS.

The fact that areas formerly occupied by heather at Walldridge and Birtley are now covered with bracken, *Nardus*, or *Ulex* has already been mentioned. Bracken similarly tends to spread into areas at present covered with various other plants, notably *Nardus*, *Deschampsia flexuosa*, and *Agrostis vulgaris*. A quantitative estimate of the rate of spread where this takes place by vegetative reproduction alone has been made. To do this it was necessary to make a permanent mark on the boundary between two associations, and to compare the boundary at a later date with that indicated by the mark. The comparison could be done most satisfactorily by photographic means, which were used in about half of the cases. On account of the number of passers-by it was impossible to use a conspicuous mark, such as a stake, for it would probably be removed; it was however found that a sufficiently permanent record could be made by cutting out a triangular sod down to the bottom of the humus. The base of the triangle was made a tangent to the front at the commencement of the experiment. When a photograph was to be taken, a portable stake was placed at the base of the triangle, and the camera was in the line obtained by producing the base. Records were made in this way in the autumn of 1914 of the positions of many points on the bracken front.

At one place opposite the beechwood where bracken appeared to be advancing into a dry *Nardetum*, with *Deschampsia flexuosa*, *Festuca rubra*, and *Anthoxanthum*, the front in June, 1915, was 70 cms. behind the previous year's position, save for one outlying frond which was 160 cms. past it. In September, the outermost shoots of the bracken had come up, with the result that two new plants were 95 cms. past the triangle. In June, 1916, the front was solid up to 15 cms. past the base of the triangle, but the outposts were not up. In September, however, they had reappeared.

The limits of an outlier of bracken, about 20 metres across, among dry *Nardetum* on the S.W. side of the Fell were recorded similarly, and indicated a spread of 70 cms. in two years. Similar results were obtained in most of the determinations made. The largest was on Hill 13, where on fairly level ground on the hill top I observed a spread of a metre in one year, and one of 2½ metres in two years.

¹ It has been observed by B. E. Livingston, *Botanical Gazette*, 39, 1905, pp. 348-355, that water from live *Sphagnum* has no toxic effect on the alga *Stigeoclonium*. The water from decayed *Sphagnum*, however, has a decided toxic effect, and it is concluded that a toxic substance is produced in decomposition. This is not however due to acidity alone. This property of *Sphagnum* appears analogous to one of those of *Pteris*.

A particularly interesting instance occurred in the disused pasture near Hill 13. The bracken appeared to be spreading down the slope, starting from the plantation, but to be stopped along a horizontal footpath some metres below the edge of the wood. In one place where the bracken was still half a metre from the path, a spread mark was made, to ascertain whether it could reach the path during the summer of 1915. Actually, on the whole front of 80 metres, this was the only point where the bracken crossed the path. The two fronds that then appeared were replaced by four in 1916.

Two spread marks were made on Beamish Fell, but the bracken advanced so rapidly that after the autumn of 1915 it was impossible to find them below the refuse.

Attempts were made to determine whether *Nardus* is extending anywhere at the expense of *Calluna*, but up to the present these have led to no result; yet the presence of *Calluna* refuse in the humus below *Nardus* has several times indicated that this has formerly occurred.

At one place where a very large *Ulex* bush was growing a record was kept of its rate of extension. The new wood produced increased the radius of the bush by 15 cms. a year. It was growing among *Calluna*; dead *Calluna* extended 70 cms. into the bush, and dead *Nardus* still further. Some distance away, dead *Calluna*, not burnt nor rotten, was found among well established bracken, showing that some of the transition from *Calluna* to other plants is very recent.

THE EFFECTS OF FOOTPATHS AND WEAR.

There are two striking ways in which the footpaths at Waldrige influence the vegetation. They are made in most cases by simple wearing: numerous persons repeatedly walking each in the track left by the last ultimately leave a definitely marked impression on the ground, and this is usually permanent. Owing to the repeated pressure, the earth tends to be pressed down and hardened on the paths, which are thus lower than their surroundings. Hence in wet weather they act as intermittent water courses, and thus tend to have a less xerophytic flora than their surroundings. Further, the frequent traffic has a direct effect on the vegetation on account of sheer mechanical wear, to which some plants are much more sensitive than others. In consequence of these facts the associations developed on a footpath are usually different from those at the sides.

Frequent trampling must evidently have a bad effect on any plant with a stiff stem. In consequence, where a path exists among such plants it can always be traced by the absence of *Calluna*, *Ulex*, and *Pteris*, which are replaced by grasses. The effect on *Calluna* and *Ulex* is purely local, but that on *Pteris* is more serious. When a patch of bracken has spread until it

abuts on a footpath, the majority of the shoots from the rhizomes sent out in the direction of the path actually rise in the path, and are soon broken. Thus bracken always finds it exceedingly difficult to cross a path. The only way it can do so is by sending out a rhizome long enough to go right under the path and send up a shoot on the other side. The plant then spreads from this outlier. This is not, however, a very common occurrence, and the wider the path the more rarely it takes place. Near the most westerly point of Walldridge Fell is a disused unmetalled road, now overgrown with *Nardus*, and for about 50 yards along it the bracken grows close to it; on the other side of the road there is no bracken, but there is little doubt that if the road had not been present, *Pteris* would long ago have invaded this part. The importance of a road or a wide footpath is then that it stops the vegetative spread of *Pteris*.

Even where a footpath is disused *Pteris* seems to find a difficulty in crossing it. The rhizomes move along on an average about 10 cms. below the surface, and the hardening due to pressure persists down below this depth. In many cases the rhizome cannot penetrate this layer, and the spread may be seriously delayed. Places where this appears to be taking place have repeatedly been observed, but the *Pteris* usually gets across in time and then spreads from the resulting outpost.

Those plants that are capable of growing on a footpath are always much smaller there than in surrounding areas. Thus in one place where a path passed through a *Nardetum* and was slightly raised above its surroundings on account of unevenness in the ground, *Festuca rubra* and *Agrostis vulgaris* were co-dominant on it, with *Festuca ovina* abundant. *Festuca rubra* on the path was 15 cms. in height, and in the *Nardetum* 75 cms. *Agrostis* was 5 cms. high on the path, and 20—30 cms. in the *Nardetum*. *Festuca ovina* did not occur off the path, and conversely *Deschampsia flexuosa* grew in the *Nardetum* but not on the path. As soon as the path became depressed below its surroundings *Nardus* and *Juncus squarrosus* became dominant on it, both being dwarfed. Where the soil is sufficiently damp for it the latter plant seems to be strongly favoured by wear. Where a footpath passes through a wet *Nardetum* or a *Molinietum*, the *Juncus* is usually abundant or even co-dominant on it, though it may be only occasional in the surroundings. *Juncus acutiflorus* is similarly favoured, but to a less extent. These plants are not so much dwarfed in these conditions as others appear to be.

At Birtley large areas of the Fell are extensively rolled on behalf of the local golf club. This naturally has an important effect on the vegetation, and is probably one of the most important causes of the succession from *Calluna* to *Nardus*. On one rolled strip, one of the largest on the Fell, and now dominated by *Nardus*, *Calluna* bark corresponding to stems 5 mm. thick was found. The tallest *Calluna* plants on the strip are only 5 cms.

high, with thin stems, and there were none at all within 3 metres of the spot examined. Just off the rolled area *Calluna* grows to a height of 15 cms., flowers profusely, and is plainly able to hold its own with *Nardus* and even to defeat it. It rarely flowers on the rolled area, which implies the ultimate extinction of a plant that does not reproduce vegetatively.

This advance of *Nardus* at the expense of *Calluna*, while *Ulex* is advancing over it from the opposite direction, leads to a peculiar result where the two invaders meet. The *Calluna* is unable to grow either in the Nardetum or under the larger *Ulex* bushes. In consequence the only place where it and its associate *Erica cinerea* can grow is among the small *Ulex* bushes, which protect it from wear and at the same time are not tall enough to smother it.

Between the bushes of the Ulicetum proper *Nardus* is generally dominant. It there grows considerably taller than elsewhere, probably because wear is absent or very slight. *Calluna* also occurs, and with it *Salix repens* and occasionally *S. aurita* and *Genista anglica*.

EFFECTS OF THE PRESENCE OF ANIMALS.

Many rabbit burrows occur on the sandier parts of Beamish Fell. The ground around them is exposed, and an open association grows, with

<i>Rumex acetosella</i>	<i>a</i>	<i>Poa annua</i>	<i>f</i>
<i>Spergula arvensis</i>	<i>a</i>	<i>Holcus lanatus</i>	<i>o</i>

The whole is surrounded by *Deschampsia flexuosa*. The superficial sand is finer than that below. Except in the immediate neighbourhood of the burrows the effect of rabbits appears to be always small; the *Deschampsia* always grows luxuriantly, although observations near the burrows indicate that they eat it in preference to all other plants.

On the part of Tinkler Fell to the north of the road rabbits are very plentiful. Some of the *Calluna* bushes take the form of convex hummocks, like those in Breckland described by E. P. Farrow¹. They are not filled with sand like many of these, but have the same characteristically regular form, owing to rabbits eating the ends of the twigs. On the main part of the Fell *Calluna* does not appear to be attacked, but hummocks of *Festuca ovina* occur, resembling the earlier stages of those of the Breck Country.

At most parts of Waldrige Fell the effects of rabbit attack are very small. On Hill 3 there are several holes, but the pressure is so slight that even close to the holes *Deschampsia flexuosa* is not noticeably shorter than elsewhere. On Hill 13, however, the effect is more important. Round the holes *Deschampsia* is eaten short. *Nardus* is also attacked. *Luzula campestris* is not much affected, and *Galium saxatile*, *Holcus mollis*, and *Agrostis vulgaris* apparently not at all. At the margin next the plantation, the rabbit attack

¹ "On the Ecology of the Vegetation of Breckland," Part II, this JOURNAL, 4, 1916, Plates VI and VII.

is still more severe; the dominant grass is there *Holcus mollis*. Apart from the rabbits, there is no very obvious reason why *Deschampsia* should not occur at this point, with possibly *Molinia* in the depressions, and it was thought desirable to test this point experimentally. Two clumps containing *Molinia*, *Nardus*, *Deschampsia*, and *Juncus squarrosus* were therefore transplanted into the *Holcetum mollis*. The next year the three grasses were all eaten short, and failed to survive throughout the summer. It was thus evident that the preference of the rabbits for the other grasses rather than *Holcus* was sufficient to destroy them and ensure the dominance of the latter, which seems to be less palatable. I have up to the present no evidence that rabbits ever eat it at all. The ends of the leaves of *Juncus squarrosus* were eaten, but it was not violently attacked, and survived and fruited.

Rabbits do not occur on Birtley Fell, probably owing to the heaviness of the soil.

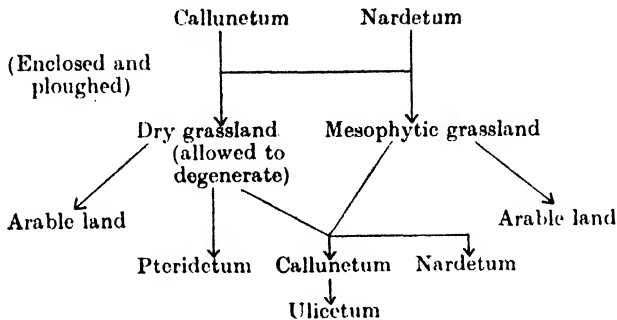
Near houses extensive manuring takes place, principally by fowls. This seems to promote the dominance of *Agrostis vulgaris*, *Poa annua*, and occasionally *Lolium perenne*.

Pasturage is not extensive. One farmer is said to feed cattle at Walldridge, and several horses are often on the Fell. A few cattle and horses are also fed on Birtley Fell at certain times. The effect on the vegetation is not however striking, and none of the phenomena yet noticed have been traced to pasturing, with the possible exception of the shortness of the grass in the *Agrostetum albae*, which is a favourite feeding ground. Some goats are kept at Tinkler Row, Walldridge; the fact that many of the neighbouring *Ulex* bushes show signs of having been nibbled at the ends of their lower branches is probably to be attributed to them.

The effect of pasturing is much more striking when a part of the Fell is enclosed for the purpose. This does not often occur, and the writer has not observed the actual successions following on enclosure in the localities considered; but on the heathland areas of East Northumberland, which are related in character, ploughing always follows immediately afterwards. The *Callunetum* or *Nardetum* of the heath at once passes to grassland, and in the absence of sowing or manuring an association of *Agrostis vulgaris* and *Festuca rubra* is soon established on dry ground, and a mesophytic *Graminetum* on damper ground. At Walldridge only the dry grassland occurs. As long as pasturing continues there is no sign of any return to primitive conditions in the absence of further ploughing. Many adventitious plants appear such as *Cerastium triviale*, *Trifolium hybridum*, *Bellis perennis*, and *Plantago* spp. which do not occur in any natural community round about. The great number of species in the dry grassland at Walldridge and part of that at Birtley is to be attributed to invasion by plants of this type, probably encouraged by the constrained shortness of the herbage. It is probable that the incidental manuring is of importance in the maintenance of the

grassland, and that still more important is the influence of mechanical wear in restricting the growth of *Ulex*, *Calluna*, and *Pteris*. When grass pasture is left to itself, it may behave in several different ways. If it is very dry it will remain practically unaltered for a long time, as in the case of the field to the north-east of Hill 13. The principal change is that the dominant grasses grow tall, and the plants of shorter stature die out. Stiff-stemmed herbs such as *Teucrium scorodonia* also increase in quantity, except on foot-paths. Bracken may later invade the area by rhizome growth; it appears to be doing so in the pasture last mentioned, and will probably become dominant. On the northern slope of Hill 12 is another degenerating pasture of a different type, with a larger water-supply. From the remains of a fence round it, and the smoothness of the ground within it, it is probable that this was at one time dug. The surrounding vegetation suggests that before that it was probably covered with *Calluna* and *Nardus*. In 1890 it was a grass pasture, and is so marked in the latest Ordnance Map. It seems to have subsequently fallen into disuse, and has now reverted to typical *Callunetum*, save for a strip of grass land across the middle which still remains. *Nardus* now fringes the ditches round the edge. At one point *Ulex* is advancing at the expense of the *Calluna*.

The successions consequent on enclosure for pasturage are then:



RUDERAL AREAS.

These differ among themselves according to the nature of the surface that has been exposed.

At the Edmondsley end of Waldrige Fell, south of the road, shallow quarries have been made for sandstone and subsequently abandoned. Clay refuse occurs there and on the steep slope at the extreme north point of the main portion of the Fell.

Near every pitshaft on Waldrige and Birtley Fells there is a heap of shale derived from the underclay found beneath the coal. There is in particular a large shale heap from the Smithydene drift at the base of the precipitous slope that overhangs it. The soil of these is largely clay, with

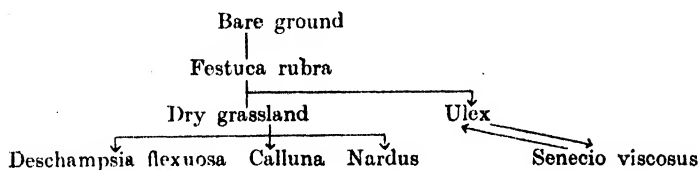
many shale fragments, which form a layer on the surface where the finer particles have been washed away. With the exception of those on the higher parts of Walldridge Fell all these shale areas are now *Uliceta*.

At Walldridge a typical list of the vegetation of such areas includes *Tussilago farfara* o, *Deschampsia flexuosa* a, *Festuca rubra* f, *F. ovina* o, *Agrostis vulgaris* a, *Anthoxanthum odoratum* f. *Plantago coronopus* occurs in a few places. Except where *Ulex* is dominant, the association is not closed. *Nardus* is dominant along the intermittent water-courses. *Senecio viscosus* is abundant where the *Ulex* has been burnt off. The driest type of these ruderal soils, occurring on steep slopes, is much colonised by *Agrostis vulgaris* and *Festuca rubra*, which also occupy the driest ground on the Fell itself. Where a ruderal soil is permanently damp, however, it is generally covered with *Poa annua*. In the case of one of the inlets to the Wanister bog, which receives part of the sewage from the village, the edge of the stream is lined with *Poa annua*, and where it spreads out at its mouth there is a rank growth of *Holcus lanatus*.

On the large pit heap on the Fell *Festuca rubra* ascends the slope to the top, although the association is not closed. *Agrostis vulgaris*, *Galium saxatile*, *Trifolium repens*, *Holcus mollis*, and *Deschampsia flexuosa* do not ascend more than two metres from the base. About halfway up there is a flourishing *Ulex* bush, with a little *Rumex acetosella* about it.

When a shale heap is very old the soil produced by the early colonists seems to lead to a growth of vegetation often very slightly different from that on an ordinary hill. On one heap at Walldridge that has not been used for many years there is now a dense growth of *Calluna*, with very few associated plants. On Hill 8, which has an ancient air-shaft at the top, there is the typical zonation with height, *Nardetum* being at the base, and passing through *Deschampsietum flexuosae* to the dry grass-heath association of *Agrostis vulgaris* and *Festuca rubra* at the top. *Plantago coronopus* occurs here. Very close to the shaft is a narrow zone of *Poa annua*.

Successions on shale heaps.



THE GROUND VEGETATION OF PLANTATIONS.

The steep banks of the two principal streams at Walldridge have been extensively planted with trees, mainly beech, oak, and pine. Though formerly

the soil was probably in no essential respect different from that of the Fell itself, the establishment of these plantations has made a large change in the vegetation. As may be expected, the ground flora is similar in type to that of natural woodland, but the number of species is very much smaller on account of the short time that has been available for colonisation. The introduction of trees leads to three obviously important changes in the ecological factors. The available light is diminished, evaporation is diminished, thus causing an increase in the water-content of the soil, and large quantities of humus are produced by decaying leaves. The first two of these factors do not appear to be very different for different trees, but the last is qualitatively different. It has already been shown that the shed needles of the pine trees are able to destroy *Deschampsia flexuosa*, on account of some toxic substance in them; this is not true of the decaying leaves of the oak.

In the plantation between the Pelton railway and the Cong Burn, most of the trees are *Quercus robur*, but there are also many pines. The greater part of the plantation is on a steep slope, while there is an almost flat area at the foot of this. The slope is partly covered with *Pteris aquilina* and *Deschampsia flexuosa*. The flat part, on the other hand, is mostly dominated by *Holcus mollis*, with *Rubus idaeus* r, *Oxalis acetosella* o, *Galium saxatile* o. Round the margin *Deschampsia* again becomes dominant, with a little *Galium saxatile*, *Rumex acetosella*, and *Calluna*. Much of the slope has no undergrowth, but the vegetation of the base is closed. It has often been observed that whereas *Holcus* grows quite close to the trunks of the oak, it does not approach those of the pine; the boundary is vertically below the extremities of the branches of the pine. The difference evidently cannot be due to variation in light-intensity, which is practically the same in both cases; further, in this country the shadow of an object is never vertically below it. The most probable explanation is that it is due to some effect of the fallen pine needles, which seem to be capable of destroying *Holcus mollis* when present in sufficient quantity, although this plant is much less sensitive than *Deschampsia flexuosa*. Larch appears to behave in the same way as pine. A case has been noticed where two pine trees were growing together, surrounded by *Deschampsia*, up to the projection of the outlines on the ground. Within this area there was no vegetation except *Pteris*, which seems to be very little affected by pine refuse, and one plant of a species of *Boletus*. Between the trees was a strip with fewer needles, the foliage overhead being thinner. This was occupied by *Holcus mollis*, with no *Deschampsia*.

Calluna only occurs at the margin of this plantation, stopping where the light-intensity is less than $\frac{1}{3}$ of that outside. In the middle of the wood the ratio reaches about $\frac{1}{15}$. Where many oak leaves lie, *Holcus* occurs oftener than *Deschampsia*, though the effect is not so decided as that produced by a small amount of pine refuse.

The pine plantation on Tinkler Fell which has recently been cut down produced in the first year after felling a dense growth of *Holcus mollis*, with some *Aspidium spinulosum*. A layer of refuse 7 cms. deep has a deadly effect on *Holcus*, but apparently less on the fern. There is at present no bracken except at one point where it is growing luxuriantly and appears to be advancing. In the third year after felling *Deschampsia flexuosa* and *Agrostis vulgaris* appeared sporadically.

In beech plantations there is little undergrowth, though small plants of *Deschampsia flexuosa* partly cover the ground, and *Vaccinium myrtillus* and *Calluna vulgaris* appear in one at Beamish; *Pteris* also occurs occasionally. In oak plantations the vegetation is much more luxuriant; *Pteris* and *Deschampsia* form most of it, *Holcus mollis* being usually found below the *Pteris*. Where the trees are very close, *Pteris* is replaced by *Aspidium filix-mas*, the change generally taking place when the light-intensity is between $\frac{1}{10}$ and $\frac{1}{15}$. Several other species also occur, such as *Lonicera periclymenum*, *Melica nutans*, *Brachypodium sylvaticum*, *Agrostis vulgaris*, and *Bromus asper*. In the mixed plantation next to the beech plantation *Agrostis vulgaris* is the dominant ground plant. *Oxalis acetosella*, *Viola sylvestris*, and *Rubus idaeus* grow with it. *Agrostis* grows close to the trunks of *Betula alba*, *Acer pseudoplatanus*, *Quercus* spp., and *Ulmus montana*, but never to those of *Pinus* and *Larix*. In the latter case the demarcation is quite sharp, and appears to be due to the refuse.

The writer wishes to express his thanks to many Cambridge botanists, for much kindness shown during the last four years; and in particular to Mr A. G. Tansley for his encouragement and interest, especially in the later stages; to Dr C. E. Moss, to whom he owes his introduction to ecology; and to Dr E. P. Farrow, a personal knowledge of whose work in Breckland led him to adopt the experimental method in his own. He is also indebted to Mr J. E. Purvis for laboratory facilities for carrying out the analyses.



EFFECT OF BURNING ON *ULEX*. On the left is an established healthy growth of *Ulex*, on which bracken is making little impression. On the right is a *Ulicetum* burnt some years ago, with charred stems still remaining. This has now been overwhelmed by bracken, and the latter will probably remain dominant.



VIEW IN A MIXED OAK-PINE PLANTATION. On the left is an oak, with *Holcus mollis* growing close to the trunk. On the right is a pine; the grass is stopped short vertically below the outline of its branches, and within this area there is no vegetation.

ON THE ECOLOGY OF THE VEGETATION OF BRECKLAND

By E. PICKWORTH FARROW

V. OBSERVATIONS RELATING TO COMPETITION BETWEEN PLANTS

(With Plate XX and two Figures in the Text)

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ON THE MANNER IN WHICH COMPETITION ACTS BETWEEN PLANTS IN MIXED ASSOCIATIONS.

Amongst the innumerable examples of isolated plants of the same species competing with neighbouring plants of different species in Breckland one of the most interesting is the case of *Juncus squarrosus* which occasionally exists in the valleys and sometimes succeeds in suppressing the neighbouring plants by means of its characteristic method of producing cup-like rosettes of strong stiff leaves which flatten out upon the surrounding vegetation and tend to kill it¹.

Plants which are more dwarf than the *Juncus squarrosus* itself are the ones which tend to suffer most from this method of suppression. *Agrostis alba* is the commonest plant in Breckland to suffer in this way, since it is often prevented by the rabbit attack from growing tall while the rabbits do not eat the tough *Juncus* leaves so readily except when the rabbit attack is very heavy. When however the rabbit attack is very heavy the taller and more vertically growing *Juncus* leaves suffer more severely from the heavy rabbit attack than do the more dwarf growing *Agrostis* leaves. They are

¹ Lindman, C. A. M., "Some cases of Plants suppressed by other Plants," *New Phytologist*, 12, 1913, p. 3.

then nibbled down closely to the surface of the soil and are unable to suppress the neighbouring *Agrostis* plants.

Sometimes dense groups of *Juncus squarrosus* plants occur, and often in these instances the central plants of a group are all dead and only the *Juncus* plants on the outer edge of the group are alive forming a sort of "Fairy Ring" of *Juncus squarrosus*. In some of these instances the death of the central plants may perhaps be partly due to some of the *Juncus* plants within the close-set colony having been suppressed by others, so that only the *Juncus* plants on the extreme edge of the colony remained alive.

The effects of the artificial experimental increase of the available water supply on the result of the competition of the various species of plants in the grass heath association have already been dealt with¹. The increase in the water supply alone enabled *Agrostis vulgaris* to grow sufficiently luxuriantly to crowd out and smother *Festuca ovina* and all its other competitors which are present under normal conditions in the grass heath association. Etiolated, dying, and dead remains of these various competitors could be found amongst and underneath the tall and luxuriant growth of *Agrostis*. In this instance, alteration in one factor alone of the environment has greatly affected the result of the competition, and has decided which of the competitors shall survive in the struggle for existence.

After having observed the details of the above instance of the way in which competition acts in Breckland, the writer examined numerous pastures with a view to finding other instances of analogous phenomena. Inside the edges of patches of taller growing rhizome-spreading grasses (such as *Poa pratensis*) in pastures, etiolated, dying and dead remains of more dwarf growing grasses, and small etiolated clover leaves on weak etiolated petioles, can often be found, while the lower portions of the stems and leaf blades of the taller growing grasses themselves are often etiolated.

In this connection it may be noted that, as is well known, many plants which in nature are very rare and only occur under very special conditions of soil, etc., can be got to grow well in gardens in very different and various soils and under very different conditions of soil moisture, etc. This is chiefly because in gardens these otherwise rare plants are protected by man from being smothered at some period of their life by various other plants (weeds, etc.), which would otherwise grow taller and more luxuriantly than they under these different soil conditions and would thus be able to smother them.

These instances illustrate the very great importance of tall and luxuriant growth of the *aerial* portions of plants from the point of view of ultimately successful competition and the extermination of competitors, and the very great importance and significance of this is often insufficiently realised, nor is it sufficiently clearly pointed out or emphasised in existing ecological literature. The fact that so many plants when protected from smothering by

¹ This JOURNAL, Part IV, 5, p. 109.

other plants can be got to grow, or at least to exist, in such very different and varied soils and under such varied conditions of soil moisture, etc. suggests that in nature different and varied soil conditions, whether dependent on the original nature of the soil or induced by root competition with other plants, have in themselves in many cases little to do with their actual *extermination*. Capability of taller growth than that of its competitors under different conditions of soil and moisture and biotic attack, etc. appears to be usually far more important to a plant for its survival and dominance and extermination of competitors on a particular area than mere differences in the soil conditions and the effects of root competition as such, and variations in the soil conditions probably act chiefly indirectly in limiting the distribution of plants and in exterminating competitors. The effects of root competition and soil conditions in these respects, though they may be very great, are probably chiefly important *because and in so far as they affect the differential capabilities of the aerial portions of various plants to grow taller and more luxuriantly than, and then to smother, those of their competitors, and in this manner to exterminate many different kinds of plants which could otherwise grow on these particular soils.*

In other words different soil conditions and the effects of root competition for nutriment greatly affect the absolute rates of growth of the aerial portions of the different competitors, but this mere retardation of growth does not in itself usually result in the death of the competitors. In affecting the absolute rates of growth of the aerial portions, however, the effects of different soil conditions and the effects of root competition thereby greatly affect the relative rates of growth of, or the race between, the aerial portions, and the resulting smothering very frequently results in the death of the competitors.

The smothering of the more dwarf *Festuca ovina* plants by the taller growth of *Agrostis vulgaris* owing to the greater capacity of taller growth possessed by the *Agrostis vulgaris* when the soil moisture was increased in the water drip experiment upon the available water supply is very interesting in this connection. No doubt the very small natural available water supply in the soil was also limiting the growth of the *Festuca ovina*, and when the small natural water supply in the soil was increased the *Festuca ovina* would doubtless also have been able to grow better than before if it were not smothered under the altered conditions of increased water supply to the roots of both kinds of plants by the *still taller* induced growth of the competing aerial portions of the *Agrostis*. In this instance the fatal result of the competition to the *Festuca* could clearly not have been the effect of root competition for nutriment *per se*, for the available water supply, and also on the manured side the available manurial supply, to the *Festuca* roots as well as to the *Agrostis* roots were very greatly increased from their previous values. It is apparently an individual case of the smothering of a plant by the taller and more luxuriant aerial portions of a competitor.

Probably the survival of many rare plants only under very special conditions in nature is chiefly because only under the special conditions of the habitat (of soil, biotic attack, etc.) can no other plant grow taller and more luxuriantly than they and thus be able to smother and exterminate them. No doubt the usual heavy mortality rate of seedlings is very largely due to their having to compete from the first with previously well-established taller growing competitors.

The view that plants chiefly and usually exterminate their competitors by competition between and smothering by the aerial portions and not by root competition for nutriment *per se* is strongly confirmed by the growth of the various plants on the experimental grass plots at Rothamsted. On the unmanured grass plots sixty or more species of plants occur, but when the supply of nitrogenous and mineral manurial constituents to the roots of all the plants is increased, and acidity is neutralised by lime, the aerial portions of about six species of plants eventually grow so vigorously as to smother practically everything else in spite of the fact that the available supply of food constituents has been increased to the roots of all plants. It is difficult to see how root competition for nutriment *per se* could usually be the effective factor in the extermination of competitors if when the available supply of nutriment to the roots of all plants is increased the number of species present nevertheless falls from sixty to six. The reduction in species consequent upon increased supply of food constituents to the roots of the plants is in some respects contrary to what might have been expected on *a priori* considerations; but the explanation chiefly is that when owing to poverty of soil and root competition for nutriment the aerial portions of no species can grow luxuriantly many species of plants then have a chance of life without being smothered and exterminated by the aerial portions of more luxuriant competitors.

The above explanation of the comparative poverty in species of the flora of rich soils that it is chiefly due to aerial smothering is probably the correct explanation of a phenomenon which has long puzzled the writer. The alluvial soil of the Holland Division of South Lincolnshire is very rich and the agriculture is very intensive, a consequence being that waste ground is comparatively small in area, and that woods and commons as ordinarily understood are practically absent. Nevertheless waste ground does occur along roadsides and in various other places, and the flora of this waste ground is very poor in species compared with that of most other parts of England.

No doubt this poverty in species of the waste ground of this district is largely due to the intensive agriculture of the surrounding region and to the absence of extensive woods and commons which could act as perpetual centres for the distribution of various plants; but the relative poverty in species on the existing waste ground seemed far too striking to be put down to this cause alone. If however it is caused by the relative luxuriance of growth of the

aerial portions of a comparatively few species of plants on the rich soil smothering the potential growth of many otherwise possible species the striking poverty in species of the wild flora of this district would be largely explained. In order to estimate the magnitude of the separate effect of the absence of woods and commons it would be interesting to compare the extents of spread of various plants from individual woods and commons on the poorer ground at the edge of the rich alluvial plain on to the rich soil and along the poorer ground respectively. It seems likely that such plants would be found scarcely able to survive or spread effectively at all amongst the more luxuriant and taller vegetation on the waste areas of the rich soil.

It appears probable that plants usually kill their competitors by so reducing the available value of some factor or factors which are limiting the metabolism and growth of their competitors that the individual competitors are eventually killed off by this reduction though they may struggle on for a time by living on their reserves. In this connection the experiments of physiologists in feeding animals on gradually reduced protein rations are interesting. Probably taller growing plants often reduce the light available for their more dwarf competitors to a value considerably below its external value so that light becomes a severe limiting or controlling factor to the metabolism and growth of the more dwarf competitors (and the frequency of etiolation among clovers and grasses supports this) and the latter are eventually killed off or rendered liable to fungal attack by the reduction of metabolism and consequent exhaustion. Limitation in the amount of various other factors to the smothered plants at different times may possibly also have a bearing upon the matter. Experiments are badly needed to settle these points.

COMPETITION BETWEEN PURE PLANT ASSOCIATIONS.

Breckland is very rich in examples of almost pure plant associations competing with one another, in addition of course to innumerable examples of the more ordinary conditions in which isolated plants of the same species compete with neighbouring plants of different species.

The chief instances of almost pure or relatively pure plant associations competing together in Breckland are represented by the following pairs of dominants—

Calluna vulgaris and *Carex arenaria*.

Pteris aquilina and *Calluna vulgaris*.

Pteris aquilina and *Carex arenaria*.

Calluna vulgaris and *Erica tetralix*.

Juncus effusus and *Salix repens*.

Some of these cases of competition between almost pure plant associations have already been mentioned, and the very important influence which the presence of rabbits exerts upon the competition has been described¹.

¹ This JOURNAL, 5, Part III, pp. 1—18.

The rabbits by attacking some plants more than others indirectly confer enormous advantages upon the plants which are least attacked—especially upon *Pteris aquilina* which is only slightly attacked—and when some plants can avail themselves fairly rapidly—such as by rhizome growth and reproduction in the case of *Carex arenaria*—of the opportunity given them by the rabbits attacking their competitors, the effect of the rabbits upon the competition becomes very quickly apparent in the resulting rapid movement of the various plant associations.

Although plants which can grow tall normally possess enormous advantages over more dwarf competitors yet it has already been mentioned that those plants which naturally tend to grow tall are usually the ones which eventually suffer most from heavy and increasing biotic attack, largely because upright growing stems attract the attention of the animals and are easier for them to eat, and because the stems of taller growing plants such as seedling trees are usually fewer in number per unit area than those of more dwarf competitors and are in consequence more readily exterminated¹.

It has already been explained that the dominance of the different kinds of vegetation on the ground occupied by their respective zones in the characteristic zoned vegetation around rabbit burrows in Breckland², and also the dominance of the same kinds of vegetation on the extensive areas occupied by the corresponding large *Calluna*, *Carex*, and grass heath plant associations of Breckland, largely depend upon and represent the result of a dynamic balance between these two strongly opposed tendencies.

Thus in Breckland the existence and dominance of the large grass heath, *Carex arenaria* and *Calluna vulgaris* associations on the ground of their respective areas ultimately depend upon the injurious effects of certain intensities of rabbit attack severely injuring the taller members of the series sufficiently to allow the more dwarf kinds of vegetation to become dominant.

In other words a small intensity of rabbit attack which is just sufficient to kill off seedling trees on an area allows the relatively dwarf *Calluna* to become dominant, a somewhat greater intensity of rabbit attack kills off the *Calluna* and allows the more dwarf *Carex arenaria* to dominate the particular area, and a still heavier rabbit attack kills off the *Carex arenaria* and allows the still more dwarf grass heath to dominate the area. If it were not for the more injurious effect of the biotic attack upon the taller plants, these other more dwarf types of vegetation would quickly become smothered and replaced by the next taller member of the series, and they would eventually all become replaced by still taller woodland.

Thus the above mentioned highly characteristic plant associations of Breckland ultimately depend for their distribution and dominance on the ground of their respective areas upon the maintenance of certain particular intensities of rabbit attack over these areas, and it will thus be realised what

¹ Loc. cit. p. 3.

² Loc. cit. pp. 10—17 and Fig. 1, p. 13.

important effects the rabbits have upon the competition and dominance of the different kinds of plants, and how—when the rabbit attack is varying—these effects result in producing rapid movements in the distributions of the various plant associations owing to upsetting and altering the ultimate effects of the extremely interesting moving balance between the two strongly opposed tendencies of greater susceptibility to increasing biotic attack and the natural advantages of tall growth.

It has already been mentioned that the zonation and distribution of the different types of vegetation on the other uncultivated areas of England which are subjected to biotic attack very likely largely depend upon and represent the effects of a dynamic moving balance between these two strongly opposed influences.

Although the ultimate dominances and the ultimate distributions of the different kinds of plant associations in Breckland depend upon varying intensities of rabbit attack, yet the actual distributions of the various associations at any time do not always correspond with the possible distributions which the rabbit attack would permit owing to some plants not being able to spread so quickly as the greater destruction of their taller competitors by the rabbits. This is seen for instance in those cases where *Calluna* heath is degenerating so rapidly to grass heath that the rhizome spreading *Carex arenaria* cannot keep pace or catch up with its degenerating competitor, so that the normally or developmentally intermediate *Carex arenaria* zone has not been able to reach or cover all its otherwise possible distribution at a given time, and part of its possible ultimate area of distribution is temporarily occupied by grass heath. *Pteris aquilina* in Breckland is nearly always in a similar condition, for it can dominate all its usual competitors in the district, and its actual distribution at any time chiefly depends upon or is controlled by the comparatively slow rate of growth of its rhizomes.

Various experiments have been made in transplanting *Carex* and *Pteris* to various places in different positions in the intermediate zones which they would probably occupy if it were not for the limited rate of growth of their rhizomes in order to see if they can grow and form migration circles in these new positions, and the results so far obtained support the above view¹.

With regard to the cases of almost pure plant associations competing

¹ It was anticipated that there might be some difficulty in getting rhizomes of *Pteris* to grow after transplanting but no such difficulty has occurred in practice. If the original soil around the rhizomes is not disturbed and the transplanting is done carefully, the *Pteris* rhizomes grow quite well in their new positions and produce healthy fronds. It is however usually necessary for the transplanted plants to be protected from rabbit attacks at first, for even though they be normally little attacked by rabbits, yet isolated in a new position they are subjected to a heavier attack per individual frond, and are at first more of a local novelty, and probably on this account they are more subjected to a process of sampling by the rabbits until they become comparatively numerous and well established.

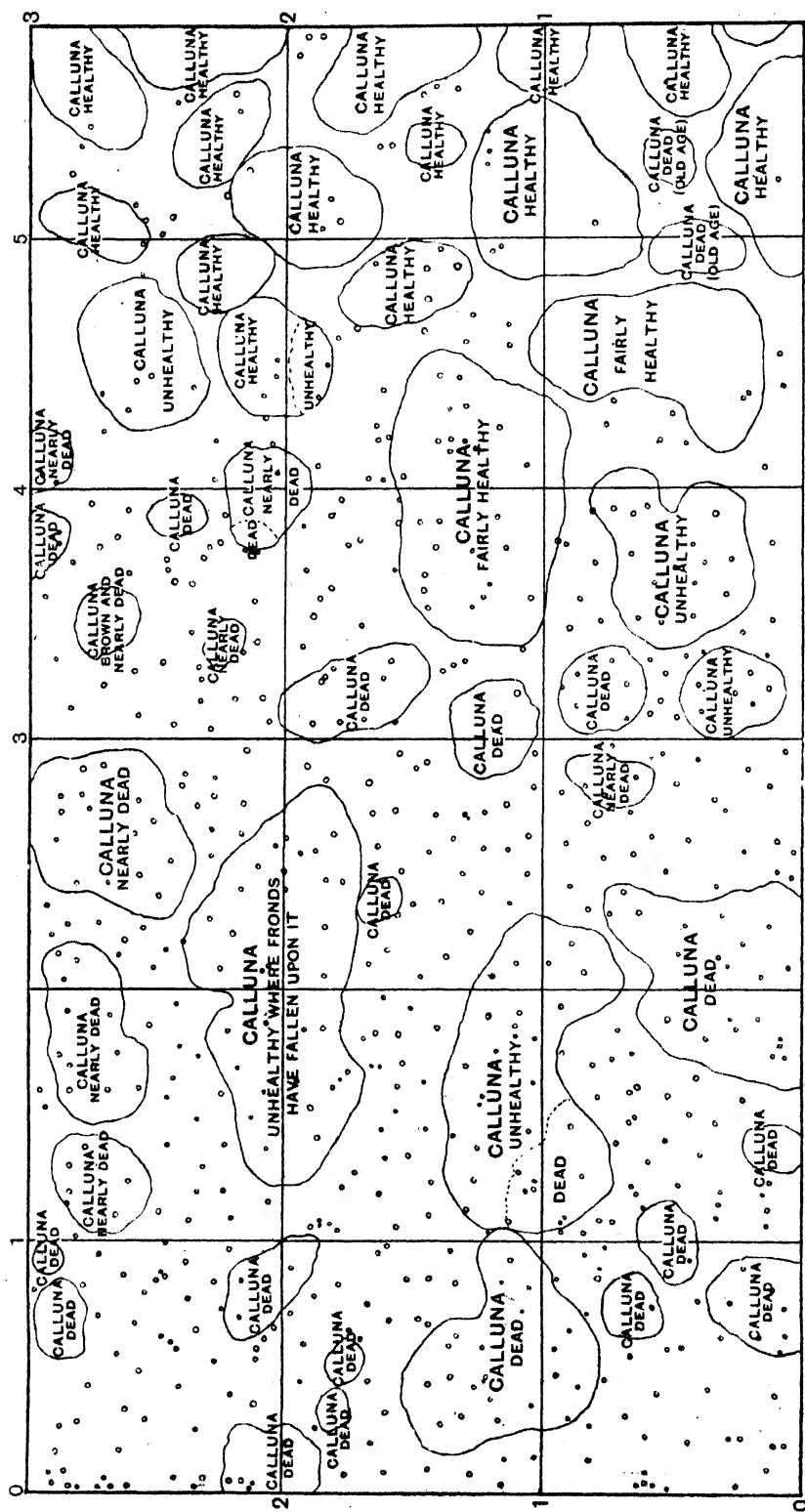


FIG. 1. CHART OF AN AREA ON THE BORDER BETWEEN A RHIZOME SPREADING *PTERIS* AND A *CALLUNA* HEATH ASSOCIATION ON CAVENHAM HEATH. The *Pteris* fronds are represented by small circles and the *Calluna* bushes by their outlines. The squares represent square metres. The *Pteris* is spreading by rhizome growth from the left-hand side of the diagram towards the right, and many of the *Calluna* bushes on the left-hand side where the *Pteris* has been for some time have been killed by the dead fallen-over *Pteris* fronds while the *Calluna* bushes on the right which the *Pteris* has only recently reached are comparatively healthy.

together under different conditions of rabbit attack in different localities in Breckland, it is frequently not known whether the two associations are almost in equilibrium in various positions or whether one of them is spreading at the expense of the other, and if so the rate at which it is spreading.

In order to obtain information upon these points many maps and charts of the distributions of the different plants on the competing zones have been made on recorded dates, such as charts of *Pteris aquilina* competing with *Carex arenaria* and with *Calluna vulgaris*, etc., and many orientated photographs of competing zones have been taken with a view to comparison with subsequent charts and photographs.

PTERIS AQUILINA KILLS ITS COMPETITORS CHIEFLY BY MEANS
OF ITS FALLEN-OVER DEAD FRONDS.

When charts of the different kinds of vegetation on competing zones between *Pteris* and *Calluna* and between *Pteris* and *Carex* associations were being made it was noticed that the boundaries between the two associations were usually very narrow, and that dying and dead *Calluna* and *Carex* plants respectively usually occurred inside the edges of the *Pteris* associations. Hence it appeared that in most cases the *Pteris* was spreading and was able to kill the competing *Calluna* and *Carex*. In an endeavour to find out the cause of this fatal effect of *Pteris* upon *Calluna* and *Carex* the root systems of the competing plants were first carefully examined. The *Pteris* rhizomes run at an average depth of 25 cms. from the surface and most of their adventitious roots are still deeper. On the other hand most of the *Calluna* roots occur between the depths 5—15 cms. from the surface, while the *Carex* rhizomes run at an average depth of 7 cms.

It will thus be seen that the *Pteris* and *Calluna* and the *Pteris* and *Carex* roots respectively occur at very different levels in the soil and that the root systems of these respective competitors might be said to be complementary¹.

It must be remembered however that though these root systems occupy different layers in the soil, yet water readily moves downwards and upwards through the soil by capillarity to any drier zone, so that these root systems although they occupy different layers in the soil probably compete effectively together for the available water supply. Not much information about the manner in which the *Pteris* was able to kill the *Calluna* and the *Carex* was derived from the examinations of the root systems of the competitors.

Another portion of a narrow transition zone where *Pteris aquilina* was competing with *Calluna vulgaris* and apparently killing it was then carefully charted in 1913, the positions of all the *Calluna* plants and *Pteris* fronds being carefully recorded (see Fig. 1). The area was also photographed so that all these records

¹ Woodhead, T. W. "Ecology of Woodland Plants in the Neighbourhood of Huddersfield," *Journ. Linn. Soc. Bot.* 87, 1906.

could be compared with other records made later on and information obtained relating to the speed with which the *Pteris* could kill the *Calluna*. When this last mentioned area was being charted the bracken fronds were in the dead winter condition, and it was noticed that the dead fronds had fallen over—apparently blown by the wind as they were all in the same direction—on to the competing *Calluna* bushes (see Pl. I, Phot. 2), and that under the blown-over dead bracken fronds the *Calluna* leaves were etiolated and often dead. In these cases where the dead bracken fronds had fallen upon only part of a *Calluna* bush it was noticed that the leaves on that portion were usually etiolated and often killed while the portions of the same *Calluna* bush where no fronds had fallen and which were exposed were perfectly healthy. Hence it appeared that the dead blown-over bracken fronds exerted a very important influence in killing the competing *Calluna*. This effect was far more marked than any effect which could be observed of root competition.

As a preliminary to later experimental investigation of the matter it was thought worth while to measure the comparative light intensities in the open and underneath dead fallen *Pteris* fronds near killed *Calluna* bushes by means of a photographic actinometer. Photographic actinometer paper even when orthochromatic is chiefly sensitive to the blue end of the spectrum while photosynthesis depends more upon the red end. In all probability a somewhat greater proportion of the light of the useful red end of the spectrum would pass through the dead brown fronds than of the blue end which latter would be that chiefly measured by the actinometer, yet nevertheless the results obtained by the actinometer might give some idea of the extent to which the dead fallen-over fronds reduced the useful light intensity. In one typical case the average actinometer time under dead fallen-over *Pteris* fronds in the neighbourhood of killed portions of *Calluna* bushes (seen in Pl. XX, Phot. 1) was three minutes, against three seconds in the open. In another case under rather dense fallen-over *Pteris* fronds the average actinometer time was eight minutes as compared with five seconds in the open. Thus the light intensity in these two cases was reduced to $\frac{1}{60}$ and $\frac{1}{96}$ respectively, of its value in the open.

It is not necessary to deduce from actinometer readings that the dead fallen-over *Pteris* fronds kill the competing *Calluna* bushes, for the effect of the dead fronds in killing the *Calluna* can be seen directly in those numerous cases where part of a *Calluna* bush has been covered by them and part has remained free.

It is not intended to infer from the above figures that the fallen *Pteris* fronds kill the competing *Calluna* bushes simply by reducing the light intensity—for example the fatal effect of the dead fronds may partly be due to retention of water and resulting decay of the *Calluna* leaves (*Calluna* leaves are delicate and readily decay). It was noticed however that the *Pteris*

fronds sometimes killed the *Calluna* leaves before the fronds themselves began to decay and it is therefore not necessary to invoke the action of a toxin produced by decay of the *Pteris* in order to account for the death of the *Calluna*¹.

Though light intensity in the open is not usually the limiting factor to photosynthetic activity, yet when it was reduced to $\frac{1}{16}$ — $\frac{1}{96}$ of its previous normal value it would probably become a severe limiting factor to the continued carbon assimilation of the *Calluna* even during the brightest parts of the day. Even with a thinner covering of dead *Pteris* fronds and therefore a less extreme reduction of light to the underlying *Calluna* the reduction might well be sufficient to lessen or altogether prevent carbon assimilation by the evergreen *Calluna* during the dull days of winter.

Calluna is well known to be intolerant of shade and it cannot exist where—in woods and elsewhere—the light intensity is reduced to between $\frac{1}{3}$ — $\frac{1}{5}$ of its external value. In view of these facts it seems probable that the shading effect is the chief factor in the death of the *Calluna* leaves by the fallen *Pteris* fronds, for, as above mentioned, they can kill the *Calluna* leaves before the fronds themselves begin to decay. *Cutting off of light and retention of water* with resulting decay of any delicate leaves with which they may be associated are probably the chief factors in the fatal effects of fallen *Pteris* fronds. The *Calluna* plants are practically always all completely killed between 5 and 10 metres inside the extreme advancing edge of a *Pteris* association.

It has already been mentioned that when the edge of a *Pteris* association is competing with a *Carex arenaria* association dying and dead remains of *Carex* can usually be found as the *Pteris* association is entered and that this indicates that the *Pteris* can usually kill competing *Carex arenaria*. The manner in which the *Pteris* was able to kill the competing *Carex* could not be discovered by an examination of the relations between the root systems of the competitors, but after the effect of the dead fallen *Pteris* fronds in killing the competing *Calluna* bushes had been observed, further observations were made upon the competition of *Pteris* and *Carex* and it was noticed that the effect of *Pteris* in killing the competing *Carex* was also due to the effects of the fallen-over dead fronds upon the *Carex* in the same way as with *Calluna*. Under dead fallen-over *Pteris* fronds the *Carex* plants were etiolated and frequently dead while neighbouring *Carex* plants upon which no fronds had fallen were quite healthy. The fatal effects of the dead fronds are even more marked on the more dwarf *Carex* plants than on the taller *Calluna* bushes.

The fatal effects of the dead fallen-over *Pteris* fronds upon competing *Carex* plants are very marked even where the fronds are fairly wide apart while they are standing upright for, when they fall right over, they may form a covering of dead fronds several fronds thick owing to the fallen individual

¹ Cf. Harold Jeffreys, "On the vegetation of Four Durham Coal Measure Fells." This JOURNAL, 5, p. 145 (this issue).

fronds then overlapping one another although they were fairly wide apart whilst vertical.

Later on when the upright living fronds grow more densely the lower covering of dead fronds becomes of course thicker, but before this time practically all the ground competitors have usually been killed off by the previously fallen fronds. Actinometer readings showed that the reduction in light intensity to the ground vegetation caused by the layer of overlapping dead fallen fronds on the surface is much greater than that caused by the upright living fronds even when these latter are growing fairly thickly.

In addition to having observed the fatal effects of dead fallen-over *Pteris* fronds upon competing *Calluna* bushes at many places in Breckland, the writer has observed the same phenomenon on Wimbledon Common. On Wimbledon Common a *Pteris* frontier—not so sharp and distinct as the Breckland ones—was advancing into *Calluna* bushes. The *Calluna* bushes which the advancing *Pteris* had not yet reached were quite healthy while most of the *Calluna* bushes on the ground which had been occupied by the *Pteris* for some time had been killed by the dead fallen-over fronds. Some small mounds covered by dead *Pteris* fronds were noticed on this area, and when the coverings of dead fronds on these mounds were raised, dead and decaying remains of *Calluna* bushes were found underneath them. Parts of some of the *Calluna* bushes in the transition zone had been covered by dead fallen fronds and the *Calluna* leaves under these were dead while the remaining exposed portions of the same bushes which had not been covered by fronds were quite healthy. Similar cases have been observed on the Greensand at Potton (Bedfordshire); also on Chobham Common (Surrey), Dersingham Common (Norfolk) and Bagshot Heath (Surrey)¹.

The writer has also noticed dead fallen *Pteris* fronds killing *Ulex* bushes near Welwyn and on Hampstead Heath. In Pl. XX, Phot. 2 (taken on Hampstead Heath) *Pteris* rhizomes are advancing towards the middle of the *Ulex* bush from the left-hand side of the picture and the fallen fronds are killing the middle portions of the bush which are underneath them, leaving living portions on each side separated by the dead middle portions as can be seen in the photo. There is a very close correspondence between the distribution of the dead *Pteris* fronds on the bush and the death of the *Ulex* leaves and branches, those covered by dead fronds being quite dead while those portions of the bush which have up to the present remained uncovered by dead fronds are perfectly healthy.

Pteris fronds usually grow much higher inside tall bushes in the *Pteris* associations than they do in the open. This can be seen for instance inside numerous *Crataegus monogyna* bushes on an area outside the eastern edge of the valley fen wood marked 8 on the map of Cavenham Heath. Inside

¹ Several friends whom the writer has told of this phenomenon have since observed instances of it in many other parts of England.

individual bushes in the *Pteris* associations the fronds often grow eight feet high, and one instance has been noted of a frond 11 feet (3.3 metres) growing out of the top of an elder bush (*Sambucus nigra*) whilst outside the bushes they are normally only between three and four feet in height.

When dead the tall *Pteris* fronds inside the bushes tend to remain entangled in the branches after the dead fronds on the surrounding open areas have fallen to the ground or been blown away. Sometimes the tall dead fronds inside the bushes remain entangled in the branches for several years and when this happens accumulations of tall dead fronds produced by several successive seasons exist entangled in the branches and these dense accumulations sometimes kill the bushes with which they are associated. The writer has observed a striking case of this phenomenon in a hawthorn bush on Wimbledon Common. The ends of the branches outside the accumulation of fronds had produced a few leaves and flowers, but inside the accumulation of dead fronds no such leaves or flowers occurred. Many of the lateral branches had decayed and the main branch was decaying and was weighted down very badly by the heavy accumulation of dead fronds.

This phenomenon of the dead parts of the plant's body killing the competitors of the plant so effectively is one of widespread occurrence and of considerable biological interest. It has probably had a considerable bearing upon the long survival and extensive distribution of *Pteris* and similar ferns in various parts of the world, e.g. *Gleichenia linearis* (*G. dichotoma*) in the Tropics.

It is hoped to make actual experiments upon the effects of the dead fallen-over *Pteris* fronds in killing competitors, and thus probably enabling the *Pteris* to spread more rapidly, by carefully charting and photographing areas on competing zones and then cutting and removing the dead fronds just before they fall over from large 20 metre quadrats on these areas for several successive years while leaving the fallen-over fronds on the remaining portions of the areas.

Juncus effusus and small bushes of *Salix repens* are competing in some of the valleys of Breckland. When the *Juncus* leaves die they normally fall over on to the ground and in these localities there is normally a stratum of dead *Juncus* leaves several inches thick on the surface. Where however a *Salix repens* bush is growing amongst the *Juncus conglomeratus* the dead *Juncus* leaves remain entangled in the *Salix repens* branches and cannot fall on to the ground. In consequence of this there is often a dense accumulation of dead *Juncus* leaves produced by several successive seasons entangled amongst the *Salix repens* branches (cf. the same thing in the case of *Pteris* and *Crataegus*) and these dense accumulations of dead *Juncus* leaves frequently kill the associated *Salix repens* bushes. In the case of more dwarf *Salix repens* bushes the dead *Juncus* leaves kill them by falling right over on top of them, for the contents of small raised heaps in the normally level deposit of dead *Juncus* leaves were examined and dead and decaying remains

of small *Salix repens* bushes were found underneath the heaped up *Juncus* leaves. This killing of *Salix repens* bushes by dead fallen-over *Juncus conglomeratus* leaves resembles and reminds one of the killing of competitors by dead fallen-over *Pteris* fronds but it is not of such widespread occurrence. These instances of dead discarded portions of taller plants falling over upon and killing more dwarf plants are instances of some special advantages which certain taller growing plants have over their less tall competitors.

A SINGLE ROW OF PINE TREES ACTS AS A BIOLOGICAL BARRIER TO THE RHIZOME-SPREAD OF *CAREX ARENARIA* OWING TO THE LAYER OF DEAD FALLEN PINE LEAVES.

A patch of *Carex arenaria* much eaten down by rabbits occurs on the grass heath association of Cavenham Heath near the spot marked 17 on the map¹. The origin of this isolated patch of *Carex* was a mystery for some time. Its presence was at first usually attributed to some edaphic difference in the grass heath at this spot and it seemed possible that this might be the true explanation and it was thought of making analyses of the soil of this patch. Eventually however the writer suddenly noticed that this large patch of *Carex* on the grass heath was opposite a fairly wide gap in a single row of pine trees which runs from the point marked 11 to near the area marked 4 on the map² and was connected with the main *Carex* area on the other side of the row of trees by a neck of *Carex* passing through the gap (see Fig. 1).

It appeared on examination that the *Carex* patch owed its existence to the *Carex* having spread through this gap in the row of pines on to the main degenerate heath association and that the *Carex* had only spread through the gap in the row of trees and had not spread through the row of trees itself. Where the row of trees was fairly continuous the otherwise advancing *Carex* was kept back at a distance of about six metres from the trunks on the other side of the row. This case of the stoppage of the spread of *Carex* by a row of pines is an extremely pretty instance of a biological barrier to the migration of a species. It seemed also that this case of trees stopping the growth of the sedge might perhaps ultimately be found to have some bearing upon the important matter of the relation of a grassland type to forest, and a considerable amount of attention has therefore been given to it.

An area 150 metres long by 75 broad along the row of pines where the *Carex* is usually stopped but passes through the gaps has been carefully mapped and charted on a large scale by the gridiron method (see Fig. 1, p. 169). Many orientated photographs of the limiting zone have also been taken in order that the area may be recharted and rephotographed at subsequent

¹ Part I, this JOURNAL, 3, p. 217.

² This single row of pine trees, which acts as a biological barrier to the *Carex*, with gaps of various widths in it, can be well seen in the background of Photos. 1 and 2 of Part IV. This JOURNAL, 5, Pl. XVII.

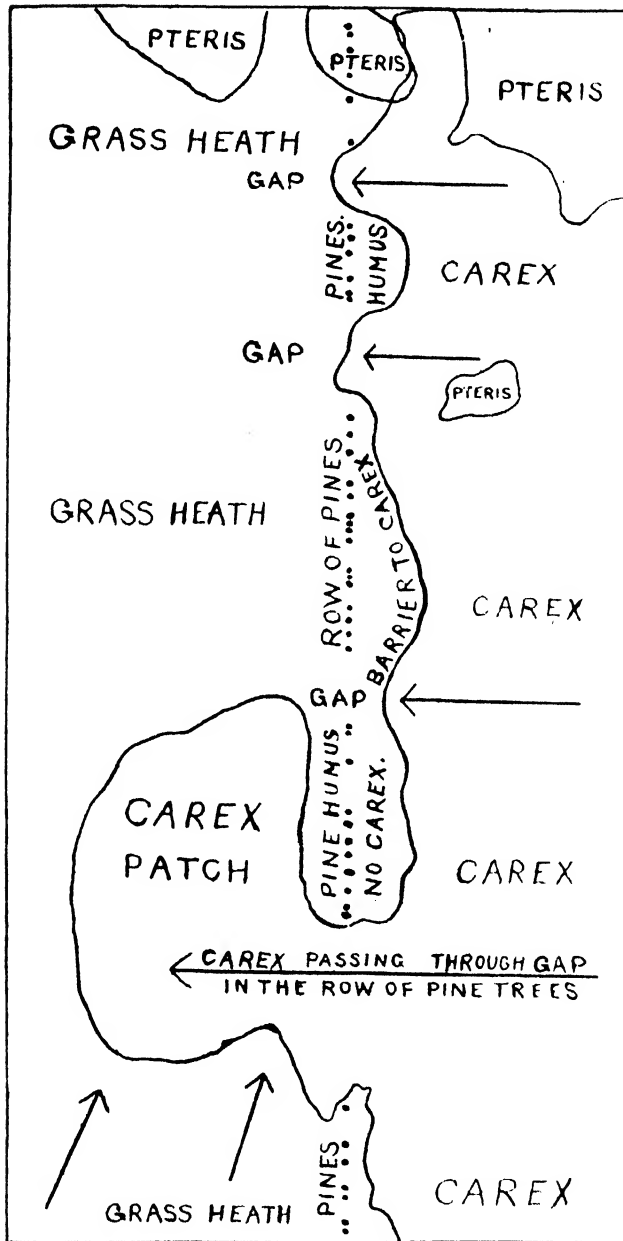


FIG. 2. CHART OF AN AREA ON CAVENHAM HEATH WHERE *CAREX AREOLARIS* SPREADING BY RHIZOME GROWTH PASSES THROUGH WIDE GAPS IN A SINGLE ROW OF PINE TREES ON TO THE GRASS HEATH BEYOND. Where the row of trees is more continuous the thickness of the layer of pine litter acts as a definite biological barrier to the rhizome spread of the *Carex* (see pages 168-172). Note that the *Carex* approaches or spreads into but not through the three narrower gaps in the row above the main gap. The *Carex* which has passed through the main gap in the row of trees forms a patch which is asymmetrical with regard to the gap. This is owing to the heavy rabbit pressure from the main area of the degenerate grass heath acting in the direction indicated by the arrows in the lower left-hand corner and keeping the *Carex* from spreading in that direction.

dates and any movement of the distribution of the *Carex* in relation to the row of pines detected and measured.

It can be seen from the chart (Fig. 2) that opposite narrower gaps the *Carex* approaches the row of pines in a uniform curve but is usually just unable to pass right through the gap. Various hypotheses to explain the stoppage of the advance of *Carex* were examined. It was thought that the stoppage of the *Carex* might possibly be due to the shade cast by the trees, but a comparison of the light reduction by the pines with the distribution of the *Carex* in various places by the help of a photographic actinometer showed that there was no definite relation between them, and this hypothesis appeared inadequate to account for the observed phenomenon. It was also thought that the advance of the *Carex* might possibly be stopped by the deposit of pine needles and cones dropped by the trees, but a general examination of the distribution of the deposit on the area revealed no clear relation between the distribution of this deposit and the stopping of the *Carex*, very many pine needles and cones occurring actually amongst the bordering *Carex*—nearly as many as on the area under the trees which the *Carex* had failed to occupy.

A careful examination of the distribution of the *Carex* in relation to each of the individual trees in the row was then made, and several instances were discovered in which the *Carex* was absent *vertically* below the branchlets on the extreme ends of certain downwardly inclined pine branches whose tips were comparatively close to the ground; although some *Carex* frequently existed between the completely bare areas under the ends of these branches and the actual trunks of the trees. In such cases the stoppage of the *Carex* seemed almost certainly due to the thicker and greater direct vertical deposit of pine needles and cones dropped down from the comparatively near branches, possibly partly combined with the shade of the branches. The deposit of needles and cones was therefore carefully removed from various of the bare areas under the ends of downwardly inclined branches, as well as from various places on the general limiting zone of the *Carex* along the row of trees, in order to see what was happening to the rhizomes which were endeavouring to invade the bare areas. It was found that as the rhizomes grew further and further under the pine branches the vertically growing *Carex* shoots and leaves became more and more etiolated until ultimately they were very yellow and weak and would not remain vertical without lateral support after the pine humus had been removed. No evidence was found of fungal attack. The *Carex* rhizomes run in the underlying sand, and as the vicinity of the pine branches is approached the deposit of needles and cones above the underlying sand becomes gradually thicker until eventually the deposit is so thick that the *Carex* shoots and leaves springing from the rhizomes cannot reach the free aerial surface, and they are completely etiolated and eventually die. The stoppage of the spread of the sedge is thus seen to be due to the thickness of the deposit of pine needles and cones dropped by the pines.

In this connection it is interesting to note that the *Carex* near the limiting edge typically grows in the form of characteristic vigorous but isolated tufts. This is probably because in this zone a few *Carex* shoots and leaves from the rhizomes in the underlying sand occasionally penetrate the above lying stratum of pine humus in comparatively weak spots resulting in the production of local isolated centres of assimilates and in the production of compact dense tufts of *Carex* shoots and leaves at these spots¹.

At the northern end of the chart (Fig. 1, p. 169) portions of an area are seen where *Pteris aquilina* has spread right under the row of trees. The bracken can spread right up to and through the row of pines even where the trees are close together, while *Carex* cannot. This difference probably chiefly arises because the *Pteris* rhizomes typically occur at a much greater depth (an average of 25 cm. from the surface) than the *Carex* rhizomes, which usually run at a depth of about 9 cms., and therefore the young coiled (circinate) *Pteris* fronds can reach the free aerial surface through a much greater thickness of overlying litter than can the young *Carex* shoots and leaves.

It is intended to experiment on the effect of pine litter on the spread of *Carex* by marking out, charting and photographing two large quadrats on this area along the limiting edge of the *Carex*. A certain depth of pine litter will then be removed from one of these quadrats and deposited evenly over the surface of the other quadrat. After a certain interval of time, the whole area will be recharted and also re-surveyed photographically, and any alteration in the distribution of the *Carex* on the experimental quadrats will be ascertained and measured and compared with any movement in the distribution of the *Carex* on the control areas at the ends.

Since the stopping of spreading *Carex* by a single row of pines was first studied on Cavenham Heath, similar phenomena have been observed in other parts of Breckland. *Carex arenaria* often grows closely around isolated pine trees² and sometimes it even grows uniformly throughout pine woods.

¹ This production of dense compact tufts of *Carex* shoots and leaves at isolated spots where the thick deposit of pine humus is locally penetrated strongly reminds one of the production of dense compact isolated tufts of vegetation on the heavily manured grass plots at Rothamsted, where the conditions of manuring are such that decomposition is retarded and a dense layer of humus remains permanently on the surface of the soil. This dense layer of humus is only penetrated by plants at isolated spots resulting in the production of the compact isolated tufts of vegetation at these points.

² In some few cases *Carex* is more luxuriant immediately under isolated pine trees than it is away from them. In one such case on Tuddenham Heath the maximum length of the *Carex* leaf blades in the open was 40 cms. whilst under some isolated pine trees the leaf blades of the *Carex* attained a maximum length of 70 cms. This is contrary to the usual condition of things, but these special reversed cases were always in valleys, and it appeared very probable that in these places there was rather more water than the *Carex* preferred, but round the pine trees the water would be reduced and the *Carex* could grow better. If this be the true explanation, these special cases of association of *Pinus* with *Carex* might perhaps be termed semi-complementary associations. The pines here help the *Carex* plants on the whole; but probably the presence of the *Carex* does not help the pines but is a disadvantage to them. If this be so these special

It frequently happens however that otherwise spreading *Carex* is absent from the area under the branches of single isolated pine trees. Such trees are usually well established and old, and in these cases there is usually a thick deposit of pine litter—sometimes over 20 cms. thick—on the areas bare of *Carex* around the trunks. The *Carex* on the limiting zones frequently grows in the form of the vigorous isolated tufts already described, and careful examination of the shoots and rhizomes which were endeavouring to penetrate the humus-covered region revealed similar etiolation and ultimate death of the young rising shoots where the overlying layer of pine humus had exceeded a certain thickness. The stoppage of the *Carex* in these instances is thus also apparently due to the thick deposit of pine litter.

It is interesting to note that the *Carex* in Breckland can usually grow quite close up to and around the trunks of most broad-leaved trees such as the oak. The writer was at first inclined to believe that this particular difference might be caused by some toxin given out by the conifer humus, but is now inclined to believe that it is primarily and chiefly if not solely due to the conifer humus acting as a far more compact and thicker mechanical obstacle to any young rising shoots which endeavour to penetrate it. The narrow pine needles and heavy cones drop comparatively vertically when they fall from the tree branches and thus they form far more definite surface accumulations of humus below the tree branches, settle down comparatively closely to the surface of the soil, are not so liable to be blown away, and form a dense compact mat around any young rising shoots at the surface of the soil. Also pine needles are not converted into humus so quickly as the leaves of most broad-leaved trees and thus they have time to form far deeper mats or accumulations on the surface. The writer is thus of opinion that it is the sheer mechanical obstacle of the thick compact, dense, impenetrable surface mat of closely packed dead needles and cones which probably chiefly causes the observed absence of vegetation under the narrow-leaved conifers. The fact that the *Carex* grows luxuriantly in the presence of much pine humus provided the latter does not exceed a certain depth, and the fact that it grows in the form of *vigorous* tufts where it has succeeded in locally penetrating an *even thicker* layer of pine humus, seem to indicate that the effect of the pine humus is simply mechanical and to exclude the existence of a definite toxic effect—at least in the case of *Carex arenaria*¹.

associations of *Pinus* with *Carex* might perhaps be termed semi-communal associations, for under these conditions the effects of competition between the *Carex* and *Pinus* plants are masked as far as the *Carex* is concerned, and the pines help the *Carex* plants. These particular associations are real semi-“communities” in some respects.

¹ Cf. **Harold Jeffreys**, “On the Vegetation of Four Durham Coal Measure Fells,” this JOURNAL, 5, pp. 152—154 and Plate XIX (present issue).



Photo 1. COMPETITION ZONE BETWEEN *CALLUNA VULGARIS* AND *PTERIS AQUILINA* ASSOCIATIONS, CAVENHAM HEATH. Note the narrowness of the zone. Dead remains of *Calluna* are found within the edge of the *Pteris* association, which is advancing and killing its competitor chiefly by the dead fronds falling on and smothering the *Calluna* bushes, as can be seen in the picture. (See pp. 163-4.) The parts of the *Calluna* bushes covered by dead fronds are usually dead, while the parts of the same bushes remaining free from the fronds are perfectly healthy.



Photo 2. DEAD FALLEN *PTERIS* FRONDS KILLING MIDDLE OF *ULEX* BUSH ON HAMPSTEAD HEATH. The rhizomes of *Pteris* are advancing towards the middle of the bush from the left of the picture. The middle of the bush, covered by the dead fronds, is dead: the portions on either side, as can be seen in the picture, are living and healthy. The correspondence between the distribution of dead fronds on the bush and the death of the *Ulex* leaves and branches is very close. (See p. 166.)



ON COMPETITION BETWEEN *GALIUM SAXATILE* L. (*G. HERCYNICUM* WEIG.) AND *GALIUM SYLVESTRE* POLL. (*G. ASPERUM* SCHREB.) ON DIFFERENT TYPES OF SOIL

BY A. G. TANSLEY

The publication, so long ago as 1865, of Nägeli's paper on the conditions of occurrence of species and varieties within their areas of distribution¹ brought into prominence an ecological problem of considerable interest and importance, namely the relation of competition between species, particularly closely related species, to their soil preferences.

The striking case of *Achillea moschata* and *A. atrata*, particularly their distribution in the Heuthal, a high alpine valley in the Bernina region of the Upper Engadine, at once suggests the investigation of this relation, but definite attempts to elucidate the problem appear to have been lacking.

Achillea moschata is a widely distributed species of siliceous soils in the Alps and is reputed calcifuge: *A. atrata*, on the other hand, is calcicole; and each, on its own soil, is said to suppress the other. But where either of the two is absent altogether from a region the other grows on calcareous and non-calcareous soils alike, though *A. atrata* is said to colonise non-calcareous soils with less difficulty than that experienced by its congener in colonising calcareous soils. In the Heuthal Nägeli found a large block of limestone, barely covered with a thin layer of soil, which had fallen on to an area of non-calcareous schist. On this block a colony of *A. moschata* had established itself, competition with the other species being excluded.

A number of pairs of closely allied species or varieties, both in the Alps and in other parts of Europe, show similar strongly contrasted soil preferences, and the relation described by Nägeli, each form being "bodenstet" where both occur and "bodenvag" where its congener is absent, appears to be common².

In order to elucidate this interesting phenomenon it is evidently first necessary to grow the two species of such a pair in competition on different types of soil and to see exactly what happens. Of a number of pairs of closely allied

¹ Nägeli, "Ueber die Bedingungen des Vorkommens von Arten und Varietäten innerhalb ihres Verbreitungsbezirkes." *Sitzungsber. d. königl. bayrischen Akademie*, 1865, p. 367.

² Cf. Schimper, *Pflanzengeographie auf physiologischer Grundlage*, 1898, pp. 115-118. See also Drude, *Die Ökologie der Pflanzen*, 1913, pp. 247-258.

species native to this country and naturally inhabiting strongly contrasted soil types, *Galium saxatile* and *G. sylvestre* proved by far the most suitable for experiment. The former is ubiquitous on light siliceous soils, the latter, absent from western Scotland, Wales and eastern England, appears to be confined to limestone hills and pastures. Where both types of soil occur within the area of distribution of *G. sylvestre*, each of the two species is very strictly confined, so far as the present writer's observation goes, to its own type of soil. For instance on the Mountain Limestone plateaux of Derbyshire the ground is often covered with a thick layer of non-calcareous chert through which the limestone crops out here and there, and in such situations the two species may be found growing within a few inches of one another, each sharply limited to its own soil. So far as observation and available records go, *Galium saxatile* does not however occur, like *Achillea moschata*, on limestone soil in the regions where its calcicole congener is absent, though it has been observed on the surface layer of non-calcareous soil which often covers the chalk to some little depth.

The experiments of which an account is given below were begun in the Botanic Garden at Cambridge by Miss E. M. Hume in the autumn of 1911 at the writer's suggestion, and continued until she left Cambridge in the autumn of 1913. They were then carried on by the late Captain A. S. Marsh until he joined the army in the autumn of 1914. Subsequent observations on Miss Hume's and Captain Marsh's cultures have been made at intervals by the writer up to the autumn of the present year, 1917.

The original method employed by Miss Hume was to sow the seeds of the two species together in deep boxes containing markedly different types of soil. The soils originally chosen were (1) a calcareous garden soil of medium texture (the ordinary Botanic Garden soil), (2) a non-calcareous and rather clayey reddish yellow garden "loam," and (3) a strongly acid peat, such as is used by gardeners for growing heaths and other strongly "calcifuge" plants. Later on (4) a natural sandy loam from an open woodland of heathy type on which *G. saxatile* is abundant was also used. Controls of pure sowings were also made on the various soils. The idea was to trace the course of competition between the two species on soils which each "prefers" in nature, and also on a soil which neither naturally inhabits.

The seeds were sown either with a seed of one species surrounded, at a distance of half-an-inch or one inch, with six seeds of the other species, or in several straight parallel rows, seeds of the two species being placed alternately in each row, so that each seed was at the distance of half-an-inch or an inch from a seed of the other species both in its own row and in the adjacent rows. The percentage germination of the seeds of both species on all the soils turned out however to be too low for this method to give the intended result. But in nearly all the experimental boxes some seeds of each species germinated, and the rapid growth of the seedlings after they became established brought the two into competition at latest during the second growing season.

The following table shows the germination percentages of the two species on soils (1) and (3).

	(1) Calcareous soil (4 boxes)		(3) Acid peat (3 boxes)	
	Range	Mean	Range	Mean
<i>Galium saxatile</i>	5 to 17	10	5 to 20	13
<i>Galium sylvestre</i>	9 to 37	22	7 to 24	15

In the fourth box of peat no germinations of either species occurred and the same thing happened in the single box of soil (2), the garden "loam."

It will be seen from these figures that while the germination of *G. saxatile* is somewhat better on peat than on calcareous soil, and that of *G. sylvestre* is better on calcareous soil than on peat, the percentage germination of *G. sylvestre* is better than that of *G. saxatile* on both these soils. In view of the small number of trials however no great reliance can be placed on this last result, especially as in one of the control cultures of *G. saxatile* on soil (4), the natural sandy loam, 38 per cent. of the seeds ultimately germinated, a percentage germination which is practically the same as the maximum recorded for *G. sylvestre* on calcareous soil.

The normal course of development is the same whether the seed is sown in the autumn, immediately after ripening, or in the following spring. Germination occurs in April and the seedlings of *G. sylvestre* come into flower on the calcareous soil in July, and fruit in August and September. Sometimes a small second crop of flowers is produced in the autumn. *G. saxatile* did not flower in any of the experimental boxes during the first year, but both species flower in June of the second year. Whether growing singly or in competition the plants cover the soil (except on peat) during the first summer and form a dense mat during the second. When the plants are allowed to flower and set seed fresh seedlings spring up where there is room between the original plants. The mats have now maintained themselves for six years from the original sowings.

BEHAVIOUR OF THE PLANTS ON THE DIFFERENT SOILS.

On the calcareous soil (1) the seedlings of *G. sylvestre* grow quite normally, but those of *G. saxatile* show marked chlorosis¹ very shortly after germination, and growth is very slow for many weeks. A considerable proportion of the seedlings succumb. Those which survive usually become normal from the third to the fifth month after germination, and when growing in competition maintain themselves for a considerable time in the midst of the continuous mat of *G. sylvestre*. Towards the end of the first growing season or at latest during the second summer the surviving plants of *G. saxatile* were overgrown by shoots of *G. sylvestre* and died, nothing being seen of them in the ensuing

¹ The terms "chlorosis" and "chlorotic" are used to designate the yellow or yellowish brown colouring of the leaves of the seedling. It appears to be the same phenomenon as is often observed in the leaves of plants other than calcicoles growing on highly calcareous soils.

spring. In one case however a plant of *G. saxatile* grew up on to the edge of the box and maintained itself there, leafing and flowering freely, well into the fourth summer. Its root was well established in the highly calcareous soil and it had a long bare stem, covered with shoots of *G. sylvestre*, terminating in the luxuriant flowering shoot system on the edge of the box. In the fourth summer during a long drought this plant died.

On the peat (3) the behaviour of the two species was very different from their behaviour on the calcareous soil. Germination of both species was slow and the plants remained small and did not flower during the first year. During the second year growth was considerably more vigorous and some plants of both species flowered. *G. saxatile* spread rapidly during the third summer (1914), forming a continuous mat over considerable areas of the soil, in which isolated shoots of *G. sylvestre* maintained themselves quite vigorously. The growth of *G. saxatile* in the peat boxes was not however so rapid and luxuriant as that of *G. sylvestre* in the boxes containing calcareous soil, and even in 1915 the peat was by no means completely covered. In the autumn of 1917 all three of the peat boxes were completely covered (except for some patches occupied by *Molinia*¹) with *G. saxatile*, among which a few quite healthy plants of *G. sylvestre* were still maintaining themselves.

On the natural sandy loam (4) the two species were sown broadcast, both together and separately. Both germinated and grew well, *G. saxatile* somewhat more vigorously than *G. sylvestre*². The former became dominant, but the latter maintained itself as isolated plants among the mat of *G. saxatile* so long as the cultures were kept (three years).

On the garden loam (2), which is not a type of soil on which either species ordinarily occurs in nature, the original experiment failed owing to lack of germinations. In the autumn of 1912 *G. saxatile* was sown, and established itself during the next season (1913). In June, 1914, a healthy tuft of *G. sylvestre* grown on the same type of soil was planted in the middle of the mat and established itself during the summer. In July, 1915, this plant was holding its own quite successfully in the midst of the mat of *G. saxatile* which had in the meantime spread over the whole box. During 1916 however the *G. sylvestre* steadily spread, overshadowing the *G. saxatile*, whose growth became less vigorous. In 1917 this process continued and by September *G. saxatile* had completely disappeared and the box was almost entirely occupied by a mat of *G. sylvestre* derived from the tuft planted in 1914. This curious reversal of dominance on garden loam in the course of the experiment requires further investigation.

¹ The large alien weeds likely to interfere with the growth of the *Galia* were consistently removed.

² In the later experiment (see p. 177) however *G. saxatile* was less vigorous than *G. sylvestre* on this soil. This curious result remains unexplained.

EXPERIMENTS TO DETERMINE WHETHER THE COMPETITION BETWEEN THE TWO SPECIES OCCURS THROUGH THE SHOOTS OR THROUGH THE ROOTS.

In 1914 Captain Marsh devised a method intended to separate the effects of root competition from those of shoot competition. Wooden boxes were constructed 12 inches long by 5 inches broad by 10 inches deep, and in the middle of each box a sheet of glass the length of the box was inserted in the soil. In two of the boxes (*S*), intended to allow of shoot competition but to exclude competition between the roots of the two species, the glass reached from the bottom of the box to the surface of the soil, completely separating the soil of the two halves. In two other boxes (*R*), the glass only just entered the soil and projected several inches above it, so that it would completely separate the shoots of plants growing on the two sides, but would leave the roots free to penetrate below the glass to the other side of the box. One *S* box and one *R* box were filled with soil (4) and the two others (one *S* and one *R*) with a mixture of equal parts of soil (4) and a highly calcareous soil. In February, 1914, ten seeds of *Galium sylvestre* were sown on one side of each of the four boxes and ten seeds of *G. saxatile* on the other sides. Controls of pure sowings were also started on the two soils. Unfortunately none of the *saxatile* seeds germinated, and all efforts to start competition by subsequent plantings failed. Accordingly in March, 1915, the writer started the experiment afresh on the same lines but with broadcast sowings. By May a full crop of *G. sylvestre* seedlings was obtained in all four boxes, and also a fair crop of *G. saxatile* seedlings. Markedly fewer of these last however appeared in the calcareous than in the non-calcareous soil. On the calcareous soil the seedlings of *G. saxatile* decreased in numbers in the two boxes rapidly and progressively during the summer.

Decrease in numbers of G. saxatile seedlings on calcareous soil.

	Root competition box	Shoot competition box
1915		
May 22	26, all chlorotic	22, all chlorotic
June 18	20, " "	14, " " but some recovering
July 11	8 " " and feeble	7, recovering but less than half inch high
Aug. 15	2, very small, one chlorotic	1, quite recovered and with long shoots
1916		
April 24	none	1, weak

Thus the direct unfavourable effect of the calcareous soil on the germination, and especially on the seedlings, of *G. saxatile*, already noted in the original competition experiments, was even more marked in this experiment in which the soil was differently made up, and led to the death of practically all the seedlings within a year.

On the non-calcareous soil *G. saxatile* made fair and quite healthy growth during the summer, but in no case were the plants so luxuriant as those of *G. sylvestre*, which in July averaged two inches in height in all the boxes. As

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usual *G. saxatile* did not flower during the first season. Some plants of *G. sylvestre* flowered in every box.

During the summer of 1916 shoots of *Galium sylvestre* spread over on to the other side of the *S* boxes, overshadowing *G. saxatile* which now showed less vigorous growth. Unfortunately nearly all the plants in the boxes on non-calcareous soil died during the late summer, probably as a result of overheating of the boxes and soil owing to undue exposure to hot sun.

This experiment is clearly not decisive as between root and shoot competition, because supposing the former to be effective, it had not sufficient time to come into play. From the records of the earlier experiments however shoot competition, supervening on the differential effect of the soil on the two species, appears adequate to account for the observed results, and this conclusion is reinforced by the later experiment. It must be noted that the samples of soil used in the later experiment, calcareous and non-calcareous alike, were evidently more favourable to *G. sylvestre* and less favourable to *G. saxatile*, than those used in the earlier experiments, and the meaning of this difference remains unexplained.

SUMMARY OF RESULTS.

1. *Galium sylvestre* germinates on calcareous soil, sandy loam and acid peat, most freely on calcareous soil and least freely on acid peat. It also establishes itself on all the soils employed, even on acid peat, though there reduced to a subordinate position. Some plants maintain themselves on peat in competition with the dominant *Galium saxatile* for at least six years.

2. *Galium saxatile* germinates on all the soils employed, but the percentage germination is on the whole lower than is the case with *G. sylvestre*. The germination rate is lowest on calcareous soils, and of the seedlings produced all become chlorotic and many die. Those which survive and become normally green do not survive competition with *G. sylvestre*.

3. On acid peat the growth of the seedlings of both species is slow. When more vigorous growth begins that of *G. saxatile* distinctly surpasses that of *G. sylvestre*.

4. On sandy loam from a heathy woodland both species germinate freely. In the first set of experiments *G. saxatile* grew more vigorously than *G. sylvestre*, when the two were mixed, and became dominant. The relations of the two species resemble those obtaining on peat, but the growth of both species is stronger during the first year.

5. On calcareous soil the growth of *G. sylvestre* is normal and vigorous from the first, while that of *G. saxatile* is very slow. All seedlings of the latter species become "chlorotic" and many die. Those which survive recover and establish themselves, but do not survive prolonged competition with *G. sylvestre*.

6. Competition appears to work through the direct suppression of the shoots of one species by those of the other as a result of the more vigorous

growth of the species which is growing on its "preferred" soil. Shoot competition acting in this way appears to be adequate as the cause of the suppression of one species by the other.

7. No evidence of root competition was found, but the experiments are not decisive against it, though the case of the plant of *G. saxatile* which flourished on the corner of the box of calcareous soil, where its shoot escaped the competition of the shoots of the dominant *G. sylvestre*, is *pro tanto* evidence against the effectiveness of root as opposed to shoot competition.

CONCLUSION.

In the case investigated, the calcifuge species (*Galium saxatile*) is heavily handicapped, especially in the seedling stage, as a direct effect of growing on calcareous soil, and is thus unable to compete effectively with its calcicole congener, *Galium sylvestre*. The calcicole species is handicapped as a result of growing on acid peat and is therefore reduced to a subordinate position in competition with its calcifuge rival, which is less handicapped. Both species can establish and maintain themselves at least for some years—on either soil. If these results are of general application they would explain the observed distribution in the case of other similar pairs of species, viz. that they are "bodenstet" where both members of the pair occur and "bodenvag" where only one occurs. Where however the handicapping is very severe, as in the case of *G. saxatile* on calcareous soils, it is unlikely that seedlings germinating on such soils would survive the general competition of the other vegetation even in the absence of plants of the congeneric competitor, and this would explain the absence of *G. saxatile* on calcareous soils in this country outside the area of distribution of *G. sylvestre*. The cause of the absence of *G. sylvestre* on the chalk of southern and eastern England is not at all obvious. Attempts to establish this species on the chalk in the neighbourhood of Cambridge by sowing seeds on bare chalk soil and in turf were without success.

No attempt was made to analyse the causes of the effect of calcareous soil on the seedlings of *Galium saxatile*, or of the effects of acid peat on the two species. Such an attempt would form the subject of an interesting investigation in physiological ecology.

THE AQUATIC AND MARSH VEGETATION OF ESTHWAITE WATER

By W. H. PEARSALL

(With twelve Figures in the Text)

INTRODUCTION.

Esthwaite Water is a small lake—less than 2 miles (3 km.) in length—lying between Windermere and Coniston, in the part of Lancashire due north of Morecambe Bay and at the southern end of the English Lake District (see Map, Fig. 1). Being a private water and relatively inaccessible, it is little known. Its altitude (65 m.) is slightly greater than that of Windermere, into which it drains.

The survey here described was carried out in July and August, 1914, and continued in August, 1915. The maps and diagrams are based on two series of continuous observations, taken during these months, and on others made in all seasons of the years 1914, 1915 and 1916.

The earlier investigations at Esthwaite were part of a general survey of the aquatic and marsh vegetation of the English Lakes. It soon became obvious that at Esthwaite the aquatic and fen successions were so complete, that a detailed survey would prove an admirable starting point for a description of the plant communities of the other lakes, and of the relationships underlying their distribution. With this aim in view, the present survey was undertaken and completed.

I. METHODS.

In surveying a definite area, adjacent to the shore of a lake, two points were chosen, both of which could be located on the 6 in. O.S. map, which was used throughout. Starting from one of these fixed points on the shore, and rowing toward the other, soundings were taken at regular intervals, until a known distance from the shore was reached. This point was also fixed and indicated on the O.S. map. Its position in relation to the shore was checked by the number of soundings taken, since these were a uniform distance apart, a distance which was known by constant practice, but which varied according to the particular wind or shelter conditions when the section was surveyed.

A heavy weighted dredger, with three hooks, was used for sounding. After a little practice it was possible to tell not only the depth, but also the

nature of the substratum, whether rocks, stones or mud. If the last, samples were taken and examined. The hooks generally brought up the plants growing at any point sounded, but as the amount of "drag" resulting from such soundings is very small, the results were always confirmed by rowing the boat back over the section again, and taking long casts to dredge up plants

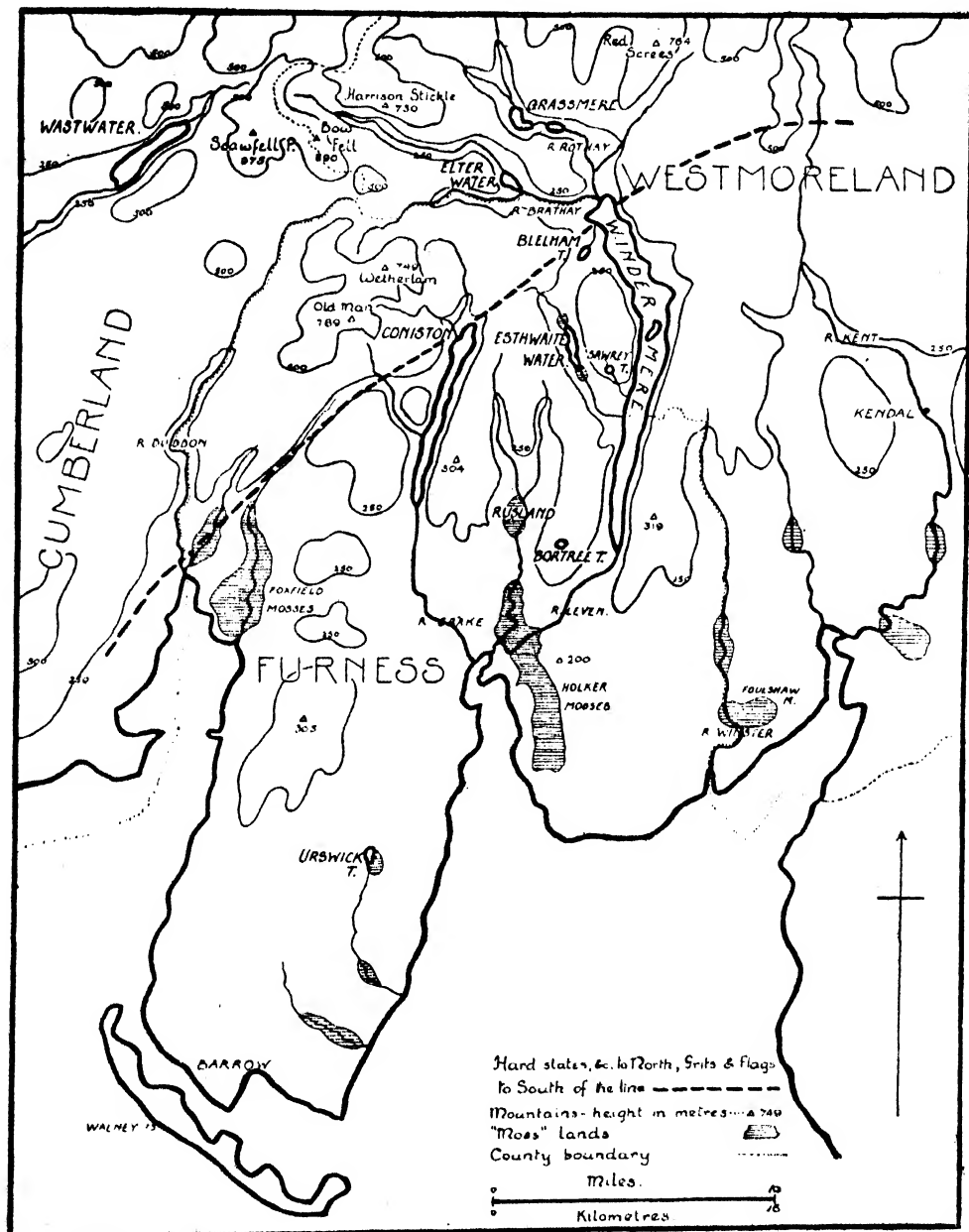


FIG. 1. Map of southern portion of the English Lake District, showing the main physical features.

along it. In this way a good idea of the plants which occurred there was obtained. When the survey of one section was completed in this way, other sections were taken with the same precautions. The general arrangement of the plant communities in the area under survey was then confirmed by scattered soundings in the regions not touched by the sections.

Subaqueous Light Intensities.

To determine the light conditions at different depths, use was made of the reaction of sulphuric acid with potassium iodide in the presence of light. I am indebted to Mr R. S. Adamson for bringing this method to my notice. It is described by Amos, in *Journ. Agric. Sci.* I, 1905. The following solutions are prepared:

1. Potassium iodide—20 gms. to 1 litre.
2. Sulphuric acid—11.5 gms. to 1 litre.
3. Potassium thiosulphate—12.7 c.c. of this solution should just decolorise 10 c.c. of No. 4 solution.
4. Iodine—centinormal solution.

10 c.c. of each solution, 1 and 2, are put into a two-ounce stoppered bottle and exposed to the light. This mixture, since it degenerates when kept, even in the dark if the day be warm, should be made immediately before use. After exposure, the quantity of iodine liberated is determined, by titrating with freshly prepared and standardised thiosulphate solution, until the liquid is colourless.

The normal degeneration of the mixture of sulphuric acid and potassium iodide was corrected by keeping control bottles in the dark and in the open air, by determining the quantity of iodine liberated, and by deducting this from the light intensity estimations obtained.

To fix the estimating bottles at the required depths, a stout cord was kept taut by a heavy weight below the water, and a wooden float at the surface. At intervals, small wire cages held the bottles from below. The air in the bottles ensured that they would always pull upward, and the surface of the liquid always stood at the same level as fixed depth marks.

One disadvantage was that the float sometimes shaded the top estimating bottle of the series, especially when this was at a depth of 1 foot (.3 m.). As the rays of the sun are oblique in England, the bottles at greater depths were not affected in this way.

Results were not obtained from a depth of 12 ft. (3.65 m.), except when a set of bottles was left out for two days (Aug. 1st and 2nd), for this purpose. A single day's exposure at this depth produced no appreciable liberation of iodine.

In the following results the estimated values are expressed as the number of cubic centimetres of thiosulphate solution required to decolorise the

exposed mixture. This value has been corrected in each case by deducting the observed degeneration of the mixed solutions, for that day. The light intensity is then found by dividing the corrected value (V) by the control value (C), obtained in full daylight on the day of the estimation.

Date and weather conditions	Depth	Corrected value (V) of estimation	Intensity = Corrected value (V) Control (C)
Aug. 1st, 1915	3 ft. (.912 m.)	.65 c.c.	.17
No wind, morning	6 ft. (1.824 m.)	.2 "	.053
bright, rain in	9 ft. (2.736 m.)	.15 "	.039
late afternoon	Control (C)	3.8 "	1
Aug. 2nd, 1915	3 ft. (.912 m.)	.58 "	.157
Weather as above	6 ft. (1.824 m.)	.18 "	.049
	9 ft. (2.736 m.)	.13 "	.035
	Control (C)	3.68 "	.1
Aug. 1st and 2nd	3 ft.	1.25 "	.17
Weather as above	6 ft.	.35 "	.046
	9 ft.	.25 "	.033
	12 ft. (3.65 m.)	.2 "	.026
	Control (C)	7.6 "	1
Aug. 3rd	3 ft.	1.18 "	.29
Very bright and	6 ft.	.28 "	.07
hot, slight breezes	9 ft.	.23 "	.057
at times	Control (C)	3.98 "	1
Aug. 4th	2 ft. (.608 m.)	.29 "	.097
Dull, close, breeze	3 ft.	.24 "	.08
light but steady	6 ft.	.19 "	.061
	Control (C)	2.99 "	1
Aug. 5th	1 ft. (.304 m.)	.28 "	.11
As on Aug. 4th	2 ft.	.18 "	.07
	3 ft.	.18 "	.07
	6 ft.	.13 "	.05
	Control (C)	2.58 "	1

The above are the only results considered in any degree trustworthy. The great variations at the same depths upon different days, which are at once obvious, may possibly be due to variations in the amount and kind of daylight. Thus bright sunlight seems to penetrate much further proportionately, than diffuse light, the changes being most marked in the surface layers of water.

In order to arrive at a more general statement of the above results, the averages of intensities recorded at given depths were calculated. From these the following figures and graphs were obtained:

Depth	No. of readings	Limits of Variation	Average Light intensity
3 ft. (.912 m.)	6	.29 — .07	.156
6 ft. (1.824 m.)	6	.07 — .046	.055
9 ft. (2.736 m.)	4	.057 — .033	.041
12 ft. (3.648 m.)	1	—	.026 (one observation)

These results, together with those of Aug. 1st and 2nd, 1915, are given on the accompanying graph (Fig. 2). The results all indicate a curve of the same general form. They show that the curve of light intensity falls very steeply

from the surface to a depth of 3 feet, that moderately high, but variable, light intensities, averaging more than .15 of the control at 3 feet, exist at depths of 3 ft. (.912 m.) and less, while below 6 ft. (1.824 m.) the curve is flat and the light is quite feeble, .05 of the control, and less. Plants occurring in these two zones must therefore live under widely different photic conditions, and may be termed *euphotic* and *dysphotic* respectively. The results of the plant survey agree very remarkably with this distinction.

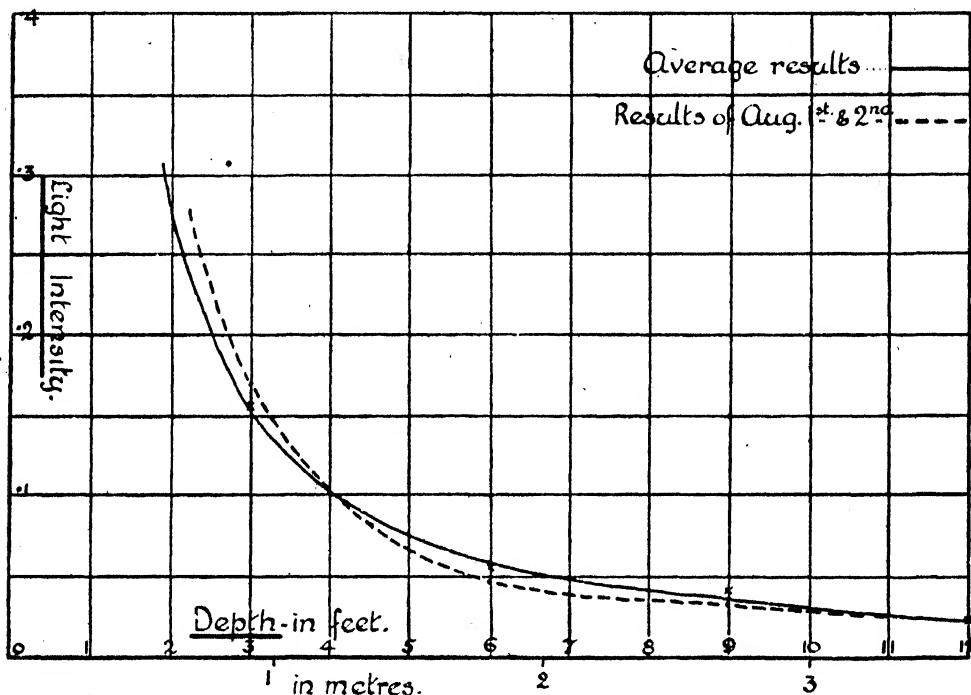


FIG. 2. Curve of light intensities at different depths in Esthwaite Water.

In addition to the light estimations, mud samples were taken. They were dried at 100° C., and then ignited to drive off organic matter. The percentage of humus was then calculated from the observed loss in weight. The samples were taken at a depth of about 5 cm., to avoid the black organic layer of mud, covering the surface of aquatic plant habitats.

II. PHYSICAL FEATURES.

Esthwaite Water (Map, Fig. 3) is about $1\frac{3}{4}$ miles (2.8 km.) in length, and some 600 yds. (547 m.) in its extreme width. It is held up by morainic material, and its three prominent points are also of morainic origin. Its shores have a more uniform character and slope than those of the larger lakes, where the underlying rock is more often exposed, and the shores are very steep. The greatest depth is in the north basin [about 70 ft. (21 m.)], while most of the middle of the lake is between 30 and 50 ft. deep (9 m. and 15 m.).

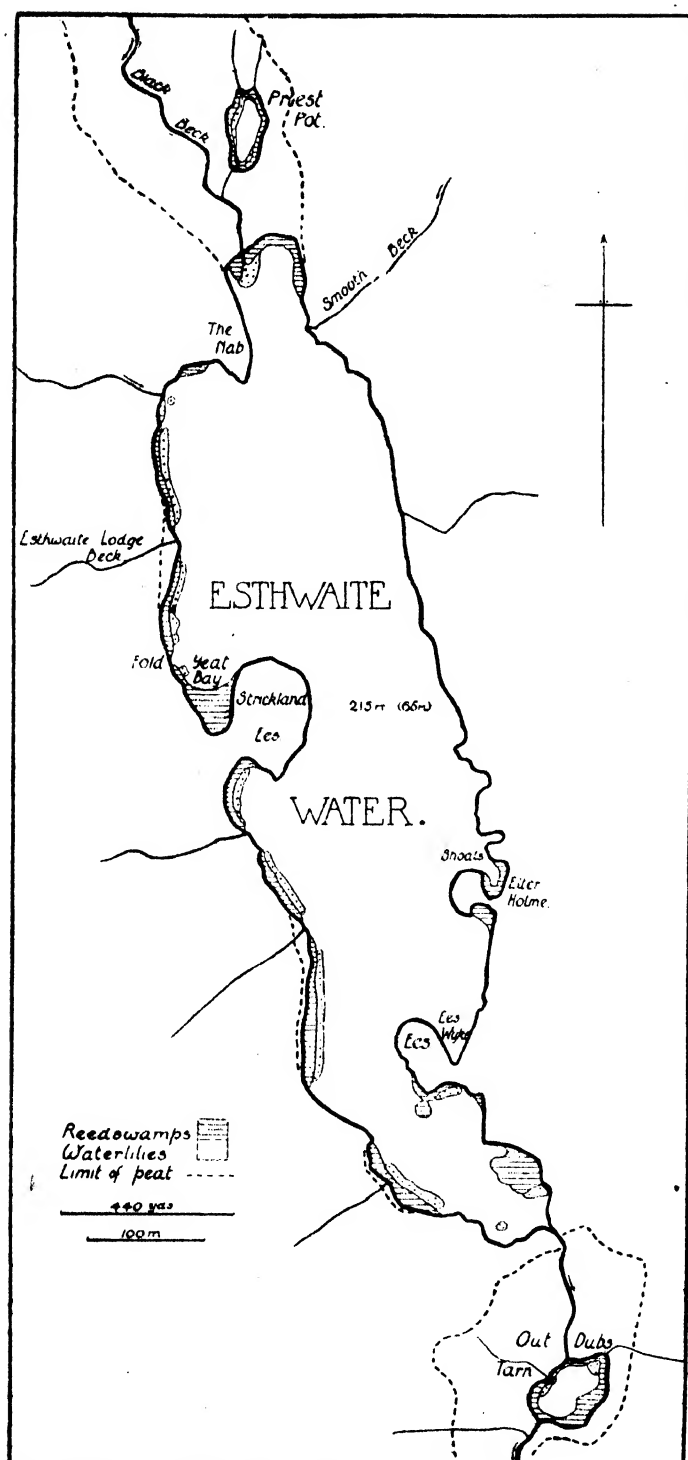


FIG. 3. Map of Esthwaite Water.

The alluvium round the lake, and the isolation of Priest Pot and Out Dubs Tarn, show that at one time the lake was about 3 miles (4·8 km.) long. Three factors contributed to this decrease in size: (i) the cutting back of the outlet, (ii) the continuous sedimentation, (iii) the invasion of the water by vegetation. Though most of the silt brought in is deposited in the lake, in heavy floods some is carried over by the outlet stream.

Composition of Water.

The water of Esthwaite is rather brown and discoloured, owing to peat in solution and suspended silt. Objects on the lake floor cannot be recognised at a greater depth than 4 ft. (1·2 m.), whereas in Windermere they are easily made out at 12 ft. (3·66 m.). The water contains more total residue than those of Windermere and Coniston, and is much more discoloured and peaty. It is acid in reaction to phenolphthalein.

Lake	Total residue	Organic residue	Hardness	Comparative acidity
Coniston	·039	·012	2·3	·2
Sawrey Tarn	·05	·014	—	·8
Bortree Tarn	·05	·015	—	·71
Windermere	·058	·019	4·0	·1
Esthwaite	·07 to ·074	·03 to ·032	3·25	1·0
Norfolk Broads	·28	·0227	23·68	—

(The figures are parts per thousand parts of water. Those for the Norfolk Broads are from *Report of Rivers Pollution Commission*, vi. 1874.)

Contrasted with the Broads, these are clearly waters poor in mineral salts. The relatively high residue of Esthwaite water is probably due to the fact that it comes from the flags and grits of the Bannisdale and Coniston series,—in contrast to Windermere and Coniston, whose main affluents flow in from the harder slates and ashy beds of the Borrowdale series (map, Fig. 1, p. 181). The more easily decomposed rocks give rise to a greater percentage of dissolved salts, and also to a greater proportion of silt in suspension. Thus Esthwaite has an advantage in this respect, although its affluents are much less in volume, and in velocity, than those of the two larger lakes.

The high organic residue and peaty colour are due, partly to the extensive area of peat north of Esthwaite Lake and partly to the more heathy vegetation on the uplands of its drainage system. Sawrey and Bortree Tarns (see map) occur on these uplands, and have a very "acid" type of vegetation. It is important to remember that the waters of Esthwaite are essentially the same in composition as these, though they contain greater quantities of silt.

The dissolved gases are not abnormal. There are usually about 39 c.c. of carbon dioxide per litre. The proportion of oxygen varies from 6·7 c.c. per litre at 7° C., in February—equivalent to about 79 % of saturation,—to almost saturation in summer.

Moulding of the Shore Line.

The forces moulding lake shores have (as will be shown) an important bearing upon aquatic vegetation. These forces depend on the size of the waves, and this in turn, on the strength of the wind and on the distance the waves can travel. Thus the height of waves is approximately proportional to the square root of the distance traversed, provided no shoals intervene.

Breaking waves are the chief agents of erosion on lake shores, and obviously their eroding power depends chiefly on their size. The matter they erode is removed by the undertow to form an extension of the terrace cut out by the waves. Thus, in the diagram (Fig. 4), *AB* is the wave-cut terrace, and *BC* the terrace formed by the eroded matter (the "*beine*"). The line *GBH* represents the original lake shore. The outer edge of the terrace (*CE*) is a bank

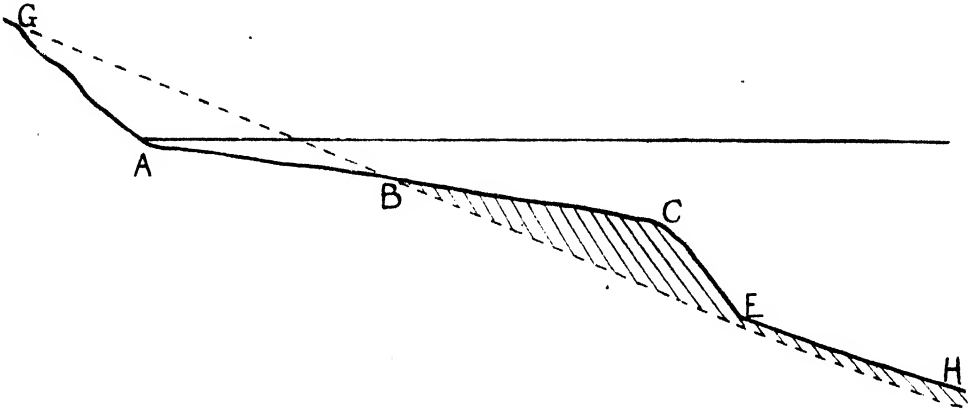


FIG. 4. Section of a lake shore, showing the moulding results of wave action on the shore line.

("mont") whose slope is 40° — 41° . [If the slope of the lake shore exceeds 40° , no *beine* (*BC*) is formed.] Only the coarser detritus is built up into a terrace; the finer sediments of erosion are carried further, and fall, along with those from the lake waters, on to the lake floor (*EH*). Thus all the primitive relief is covered, and only gentle slopes and plateaux are left.

Besides this erosion, a current is developed along the shore. If the original lake floor is left exposed at any place, this may be taken as a sure indication of slopes exceeding 40° , or else of a strong littoral current, preventing the deposition of silt. Most points and shallows on a shore are kept free from silt by this littoral current. When the current passes into deeper water, as at the entrance to a bay, it slows down, and deposits its silt. Thus bays and holes tend to get silted up, while points and shallows tend to be kept clean.

Hydrodynamic forces in Esthwaite are naturally less vigorous than in the larger lakes. Prevalent winds blow somewhat diagonally, owing to the configuration of the land, and this, coupled with the smaller size, ensures much smaller waves than in Coniston, where they have a clear sweep of nearly

7 miles (11.2 km.). Three observations, however, warrant us in assuming wave action to have considerable power in Esthwaite Lake:—(i) wave-cut terraces are frequent; (ii) reed-swamps and water-lilies are absent along the exposed eastern shore, notwithstanding their abundance along the sheltered western shore; (iii) there is an increase in turbidity along the shores on wild days, indicating that erosion is taking place.

Rough weather waves are about 9 ins. (22 cm.) in height, and probably never exceed 1 ft. (29.4 cms.). This is confirmed by the observations of Cornish, who records maximum waves of 5 ft. (1.47 m.) in height on Coniston Lake, but regards 3 ft. (.912 m.) as more usual in wild weather. Applying the law that the height of waves is proportional to the square root of the distance traversed, we get for Esthwaite a value of approximately 9 ins. (22 cms.), assuming a wave sweep of .5 mile (.8 km.), as against one of 7 miles (11.2 km.) on Coniston.

Wave-cut terraces occur along almost the entire shore-line, even on the exposed points of the western shore. They are usually more clearly marked below than above water. A rise of about 9 ins. (22 cms.) in the lake level, consequent upon the construction of a sluice at the outlet a few years ago, accounts for this feature. The outer edge of the terraces is very uniformly 3 ft. (.912 m.) below the summer water level, and the “*mont*” slopes suddenly to 4 or 5 ft. (1.19—1.47 m.). On account of this we may confidently assume that water forces are set up capable of moving fine gravel to a depth of 3 ft. (.912 m.) and finer sediments to still greater depths. In three places on moderate slopes, bare stones exist to 7 or 8 ft. (2.1—2.38 m.), and it seems probable that the water movements can remove the finest sediments to this depth. Usually, bare stones do not occur below 6 ft. (1.82 m.), unless the slope exceeds 40°. Most of the eastern shore, to this depth, is composed of the primitive rounded morainic stones, or if more exposed, is gravel. The lake floor below 6 ft. (1.82 m.) is normally, in varying degrees, silted.

At the north end of the lake, and for a short distance round the mouth of all affluents, silting is very rapid, the silt being deposited from the contributory waters. This deposition is most marked in the case of the Black Beck, the largest of the affluents. We can therefore distinguish three types of substrata in Esthwaite Water, which of course merge into one another.

1. Substrata composed of rock, gravel, or rounded stones, where sedimentation is prevented by slope, currents, or active erosion.
2. Substrata where silting is in slight excess of the disturbing factors, and a layer of inorganic silt is formed.
3. Substrata where sedimentation is rapid and practically independent of disturbing factors.

III. THE PLANT COMMUNITIES OF ESTHWAITE WATER.

The chief plant communities observed in Esthwaite Lake, omitting at present their habitat and genetic relationships, are grouped below according to their growth form, and the characteristics of each are described.

- | | |
|--------------------------------|--|
| A. <i>Rosette Type</i> | 1. <i>Littorella-Lobelia</i> associes |
| | 2. <i>Isoetes lacustris</i> consocies |
| B. <i>Elodeoid Type</i> | 3. <i>Myriophyllum alterniflorum</i> consocies |
| (all submerged) | 4. Linear-leaved associes |
| | 5. <i>Nitella flexilis</i> consocies |
| | 6. <i>Fontinalis antipyretica</i> consocies |
| | 7. <i>Sparganium minimum</i> consocies |
| C. <i>Floating Leaved Type</i> | 8. <i>Castalia alba</i> consocies |
| | 9. <i>Castalia minor</i> consocies |
| D. <i>Reedswamp Type</i> | 10. <i>Phragmites-Scirpus</i> associes |
| | 11. <i>Carex</i> spp. associes. |

The above nomenclature of plant communities is that of Clements (2) applied to aquatic vegetation, while the specific names agree with the London Catalogue, Edition 10.

1. The *Littorella-Lobelia* associes contains only the two species after which it is named—*Littorella lacustris* and *Lobelia Dortmanna*—and occurs usually at depths of from .3 to 1.2 m. but occasionally to 2 m. Hence the associes is *euphotic*—the light intensity rarely falling below .1. The community is found on gravelly substrata, sometimes overlaid by 3 or 4 cms. of black peaty mud, but never by inorganic silts. This is due to the fact that substrata at such depths are exposed to vigorous wave action, which not only prevents the accumulation of inorganic sediments, but also makes the substrata unstable. Once colonised by families of *Littorella*, the gravel is increasingly stabilised as colonisation becomes more perfect. Finally, a sward of *Littorella* and *Lobelia* completely stabilises the substratum—in the interstices of which silt and plant remains are caught—so that the subsequent formation of soil is more rapid. The chief agent in the colonising stages is *Littorella*—single plants of which are rooted up by ducks and washed on to exposed shores—because its long rooting shoots enable a single plant, once established, to extend vegetatively and form families. *Lobelia*, with no vegetative reproduction, but only small seeds, comes in when the *Littorella* communities are sufficiently advanced to arrest seeds and silt among their leaves and roots.

2. The *Isoetes lacustris* consocies is developed on primitive rounded stones at depths of 1.5—2.7 m. It is, therefore, *dysphotic* (light intensity .06—.03). Silt is absent, though a very thin black peat may collect. The consocies occurs here only at the extreme south of the lake, before reaching which, almost all the fluvial silt has been deposited. The occurrence of this consocies in the larger lakes confirms the above description of its habitat.

3. The *Myriophyllum* consociates occurs in a zone between the above communities, along the foot of the "mont" at a depth of approximately 1.25 to 1.5 m., forming a narrow zone chiefly along the eastern shore. It is found in exposed places where no other vegetation exists, and represents the most favourable plant habitat in such exposed situations, the outer edge of the wave-cut terrace containing the finest materials included in it. Shorewards there is unstable wave-swept gravel; deeper, are bare stones devoid of silt. It seems probable that the well-developed root system and finely cut leaves of *Myriophyllum* are of value in affording, respectively, secure anchorage and minimum resistance against wave-wash. Its leaves are normally just below the surface, hence the community is *euphotic*.

Myriophyllum alterniflorum is usually the only plant, but in later stages, *Potamogeton alpinus* and *Potamogeton heterophyllum* var. *longipedunculata* (Mérat) are found—the former on the sheltered west, the latter on the exposed east shore of Esthwaite. For this position the variety is well adapted, as it develops a thick carpet of small vegetative shoots close to the substratum, and sends up a few attenuate flowering shoots with stout long peduncles and no floating leaves. It occurs in the Great Lakes of North America in similar positions.

Apparently these communities of *Potamogeton* are Clements's *sociés*, since the pondweeds are dominant over a portion of the area delimited by the *Myriophyllum* consociates.

4. The linear-leaved associates includes two phases—dominated by *Najas flexilis* and *Potamogeton pusillus* (agg.) respectively. The full list of species is as follows, the characteristic ones being asterisked:

<i>Potamogeton perfoliatus</i>	r.	* <i>Najas flexilis</i>	ld.
<i>P. crispus</i>	vr.	* <i>Callitriche autumnalis</i>	lab.
* <i>P. crispus</i> var. <i>serratus</i>	o.	* <i>Elodea canadensis</i>	f.
* <i>P. obtusifolius</i>	l.	* <i>Hydrilla verticillata</i>	
* <i>P. pusillus</i>	lab.	• var. <i>pomeranica</i> Casp.	f. (7)
* <i>P. pusillus</i> var. <i>tenuissimus</i>	ld.	<i>Myriophyllum alterniflorum</i>	l.
* <i>P. Sturrockii</i>	ld.	<i>Nitella flexilis</i>	l.

This community develops best in depths of 1.5—2.6 m., and is therefore *dysphotic*—light intensity .06—.03. The remarkable uniformity in the vegetative type of the characteristic species is very striking. All have the pellucid linear leaves and delicate stems of the *Potamogeton pusillus* type. The elongate sub-species *P. Sturrockii* has this character still better marked; the variety *serratus* of *P. crispus* is bright green and translucent; *Hydrilla verticillata* is represented by one of its slenderest varieties; and the peculiar elongate form of *Elodea canadensis* also closely approximates to the type form of the community. The uniform light conditions under which the associates develops, have probably a direct influence on its growth form; yet light does not entirely

control its distribution, for it is found only where the mud is inorganic—blue-grey in colour and clayey in texture—having less than 15 % of organic matter.

The *Naias* consociates occurs on the purer silts, merging gradually into the full associates as the organic content increases. Samples from this consociates gave respectively 8.9, 7.7, 7.0, and 5.5 % of organic matter, while from the full associates, the organic contents were 14.7, 14.6, 13.9, 13.2, and 12.1 %. (Intermediate samples from transitional communities are omitted.)

It is remarkable that *Naias flexilis* is the only member of the whole associates which fruits abundantly and is dependent on seeds for its dispersal. The other characteristic species rely mainly upon vegetative means of reproduction, and with occasional exceptions, have not been seen in fruit in Esthwaite. Probably the multitude of seeds produced by *Naias* enable it to colonise newly deposited inorganic substrata before its associates in this community. On the other hand, vegetative reproduction seems more certain, and *Naias* may be ousted through this cause, once other species are established. Of the members of this associates, *Potamogeton pusillus* (agg.) and *Callitriche autumnalis* have perennial rhizomes; *Hydrilla*, *Elodea*, and *Myriophyllum* have gemmae buds and *P. crispus* has hibernacula.

The fragile growth-form and the need for inorganic silts, both indicate that shelter is of great importance in the development of this associates. Exposure to water movements would injure the plants, and prevent the deposition of silt.

5. The *Nitella flexilis* consociates occurs on similar mud, but with a greater organic content—average 16.9 %. (Samples: 18.3, 17.5, 16.9, 16, 15.8 %.) The surface layer of the substratum is indeed black, semi-liquid, and foetid, but the *Nitella* runners usually occur just below this. Developing typically at depths of 1.8—3.6 m., the community is hence *dysphotic*—light intensity .05—.02. Its smaller light requirements enable it to form a fringing zone, below the linear-leaved associates, and on silts of the same organic content (10—15 %). It is also developed where silting is slow, and the linear-leaved associates, consequently, is almost or quite absent.

6. Closely allied is the consociates of *Fontinalis antipyretica*, which although typically pure, has similarly *Elodea canadensis* and *Potamogeton obtusifolius* occasionally associated with it. This consociates is found on substrata with higher organic content, as four samples, respectively 18.3, 18.9, 19.0, 19.3 % gave an average humus content of 18.9 %. The occurrence of this consociates in Esthwaite is near the mouths of the four becks on the western shore, and less luxuriantly, near the two boathouses on that shore. At these embouchures, the mud is always much mixed with dead leaves and twigs, while the water is much better aerated through the influx of a running stream. These factors, rather than the variable light intensity (.06—.02), probably determine the distribution of *Fontinalis*, a frequent habitant of streams.

7. The *Sparganium minimum* consocieties is another community of organic soils, the average organic content being 22.4 %. (Samples: 23.6, 22.8, 22.4, 22.0, 21.3 %.) All round the shores, wherever there is a well-established *Castalia alba* community, one finds outside it a zone of loose grey or yellow-grey mud, composed chiefly of small fibrous plant remains. On this grow scattered plants of a small submerged form of *Sparganium minimum*, less frequently *Potamogeton obtusifolius*, and rarely, *Elodea canadensis*. While the community is usually developed at depths of 2.4—3 m., it occasionally occurs at 1.2—1.8 m., and, therefore, light intensity is probably less important to it, than the organic substratum.

It is worthy of notice that *Potamogeton obtusifolius* and *Elodea canadensis* may occur as associates of different dominants, on substrata whose organic contents range from 10—25 %.

8. The *Castalia alba* consocieties is the most widely distributed of the floating leaved communities in Esthwaite, and includes the following additional species: *Nymphaea lutea*, lf. (near beck mouths); *Castalia minor*, o.; *Lobelia Dortmanna*, l.; *Ranunculus peltatus* and *R. truncatus*, r. (non-flowering). As the map (Fig. 3) shows, this consocieties is characteristic of the more sheltered reaches of the western shore, and its comparative absence from the eastern shore can only be due to the lack of protection from wave-action there. Where shelter occurs on that shore, there also water-lilies and reeds appear.

The organic content of the substratum is high, for four samples—23.0, 23.2, 23.4, 24.6 %—gave an average of 23.5 %. Light intensity is possibly of indirect importance in limiting the growth of leaves from greater depths than 2.5 m. (L.I. .04), which marks the outer limit of the consocieties.

All floating leaved plants probably find shelter a mechanical necessity. In this consocieties, it has probably also an effect on the nature of the substratum. Conard (5) states from nutrition experiments that abundance of nitrates is a necessity in the cultivation of water-lilies. An examination of the substratum in this consocieties shows that the organic content is very low, considering the luxuriance of the vegetation. We must therefore assume the rate of decay to be very high—an assumption borne out by the great volumes of gas given off when these substrata are disturbed. Rapid decay can only be brought about in the presence of abundant bases. Since Esthwaite water is poor in dissolved minerals bases can only come from silts, and for the deposition of these shelter is a necessity. Hence shelter is of great importance in the development of this consocieties.

9. The *Castalia minor* consocieties occurs in shallower water—usually less than 1.2 m.—on black, peaty mud, whose organic content is over 30 %. This mud lies on stones, and is rarely more than 5 cm. thick. The habitat—being in the region of wave-action—is characterised by absence of silt, and the organic matter which accumulates consequently lacks bases and, with the acid water, prevents the action of refuse-destroying organisms (West, 16) and

nitro-bacteria (Jost, 9, p. 226). Probably, therefore, scarcity of nitrates is the factor distinguishing this habitat from that of the *Castalia alba* consociates, and this assumption is borne out by the distribution of *Castalia minor* in "acid" upland tarns.

10. *Phragmites-Scirpus* associates. This is the characteristic reed-swamp, with *Scirpus lacustris* dominant toward open water and *Phragmites* toward the land. Since this associates is absent from exposed places, it is dependent on shelter and hence on a stable substratum. Neither of the associates occurs on loose gravel or on the primitive rounded stones of the lake shores. If gravel is stabilised, as by a *Littorella* sward, *Phragmites* usually spreads. The substrata are most often organic, though not necessarily peaty, containing 30—60 % of humus. *Phragmites* occurs at depths of less than .92 m., but *Scirpus* may extend to 1.3 m. The position of the latter on the outside of the reed-swamps may be due to this, or to its power of germinating under water. Its smooth, elastic shoots are more suitable for withstanding wind exposure than the stems of *Phragmites*, and so exposed reed-swamps are often composed of *Scirpus* alone.

Typha latifolia is locally dominant at the mouth of Black Beck where there is abundant marsh gas in the mud. West (16) also remarked the co-occurrence of this plant with the gas, which is evidence of rapid decay, in this case caused by the abundant silt brought down by the stream.

11. The *Carex* associates is infrequent and confined to the south end of the lake where silt is less abundant. Developed in relatively exposed places, the mud is naturally peaty and poor in inorganic matter, while the organic content probably always exceeds 60 %. *Castalia minor* is often co-dominant on the outer edge of the community, in which the following species occur:

<i>Carex lasiocarpa</i>	lsd.	<i>Equisetum limosum</i> f.
<i>C. inflata</i>	lsd.	<i>Lobelia Dortmanna</i> o.
<i>C. vesicaria</i>	a.	<i>Castalia minor</i> o.
<i>C. inflata</i> × <i>vesicaria</i> a.		

Closed reed-brakes are not usually formed here, and the observed spreading of *Phragmites* seems to show that this associates is transient in Esthwaite. Its presence indicates, however, the affinity which this lake bears to "acid" upland tarns.

IV. AQUATIC PLANT SUCCESSIONS.

The inter-relationships of the communities described above can best be followed by reference to the large scale maps (Figs. 5, 7 and 8). Fig. 5 shows the region of the most prominent point on the western shore.

Starting from Section 11 and passing to Section 3, there is a complete transition in the chemical and physical nature of the lake floor. At Section 11 the lake bottom is composed of bare rounded stones, almost devoid of sedi-

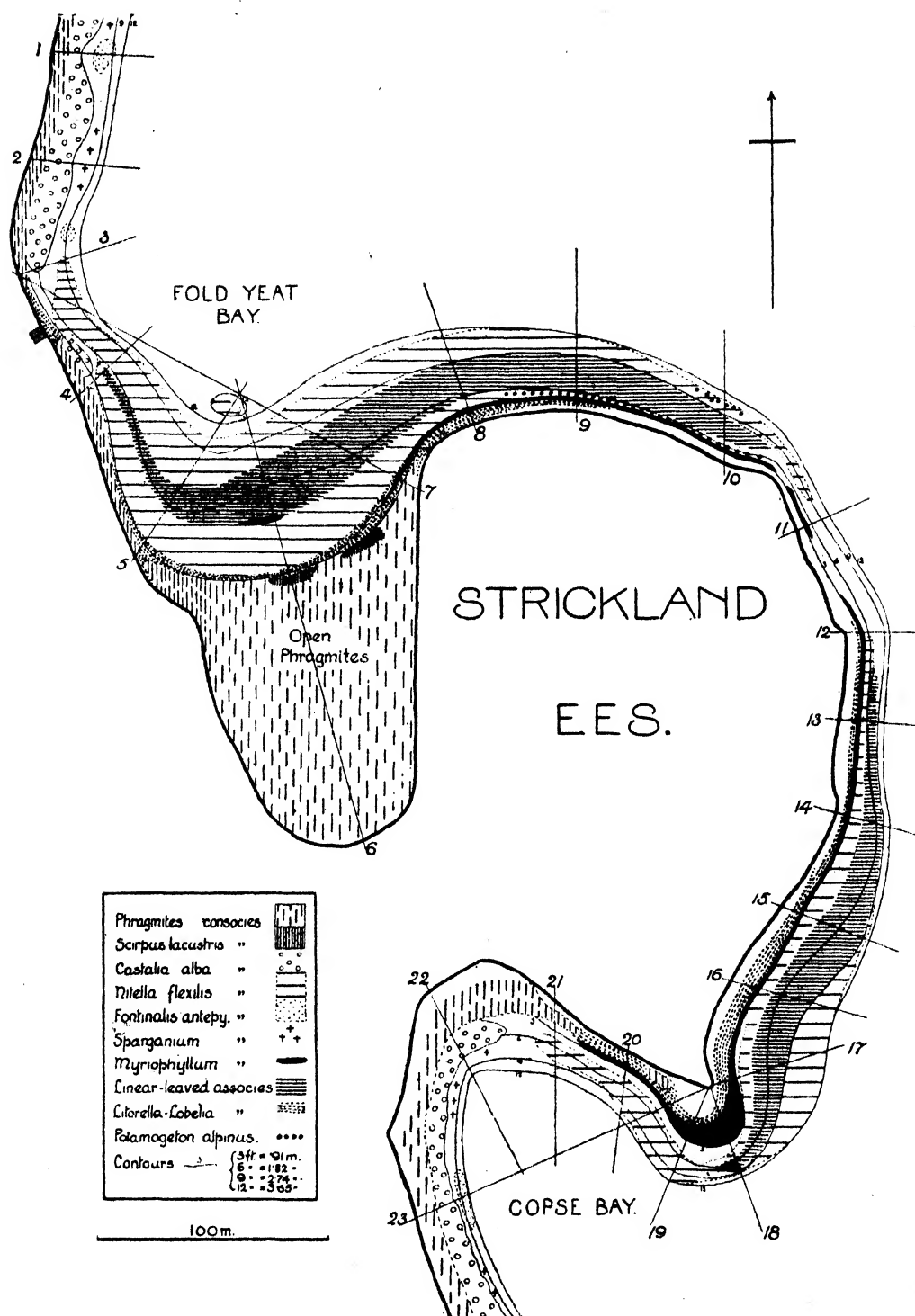


FIG. 5. Map of the aquatic plant communities round Strickland Ees.

ment; at Section 3, there is a loose grey-brown silt containing over 22 % of organic matter. While the difference in chemical constitution can only be due to plant colonisation and decay, the difference between silt and stones is due to the shelter in the bay, and consequent absence of wave-action. Silt would be deposited earlier in the bay, and also more rapidly. The point, in contrast, is relatively exposed, has a steep slope (unfavourable to silt-accumulation), and is thus silt-free. The west of this bay has thus received more inorganic silt than the exposed point, yet its substrata are more *organic*. Clearly the bay must have been colonised by plants for by far the longest period, and it follows that the communities on the west of the bay must be genetically ancient, while those towards the point are by comparison recent. The proximity of the latter to bare, uncolonised stones, and the fact that the inorganic silts at 9 and 10 are identical with those from the depths of the lake where no vegetation exists, confirm this conclusion. Further, the only closed reed-swamps and water-lilies occur on the sheltered west. By starting at 11 and going west, we can thus reconstruct the aquatic succession:

More than 1.8 m. in depth.	Less than 1.8 m. in depth.
1. <i>Naias</i> consociés	<i>Myriophyllum</i> consociés passing
2. Linear-leaved associés	into 3
3. <i>Nitella flexilis</i> consociés	<i>Littorella-Lobelia</i> associés passing
4. <i>Sparganium minimum</i> consociés	into 6.
5. <i>Castalia alba</i> consociés	
6. <i>Phragmites-Scirpus</i> associés.	

The organic content of the soil increases gradually in this transition, and the surface of the soil is raised. Thus in the linear-leaved associés, the depth at first is 2.1—2.5 m. (Section 9), but finally (Section 5), 1.6—2.1 m. As the map shows, this results in the formation of a plateau, with a steep slope outside the depth of 2.4 m. (Sections 1, 2 and 4). This plateau is colonised by the *Castalia alba* consociés and the abundant plant remains resulting develop the plateau further. We can thus account for the sudden slope of the lake floor outside a belt of water-lilies, and the slope is so steep that its surface is unstable, a fact which probably accounts for the sparseness of the *Sparganium* consociés on it. The condition of the communities at this stage is illustrated in Fig. 6, Section I. Since progress outwards is obviously very slow, the communities extend chiefly along the shore. Since, also, the level of the *Castalia* terrace is raised more quickly than it is extended outward, reed-swamps rapidly replace *Castalia*, and the final condition is that shown in Fig. 6, Section II, in which water-lilies are almost or quite absent, and outward progress of these communities has almost ceased. This condition is common in waters long colonised by plants, and is exemplified at Esthwaite, in Out Dubs and Priest Pot tarns.

The area to the south of Strickland Ees shows the same general succession as in Fold Yeat Bay. The communities in Copse Bay have nearly reached

their climax, without succeeding in passing the exposed point. In the shelter of this point, there is an area of the linear-leaved associates extending at both ends (where *Potamogeton Sturrockii* occurs), with *P. pusillus* var. *tenuissimus* dominant on mud with an organic content rather higher than the normal.

The manner in which *Myriophyllum* forms a line along shore is clearly shown, and the invasion of the extensive south-eastern shallow by this plant

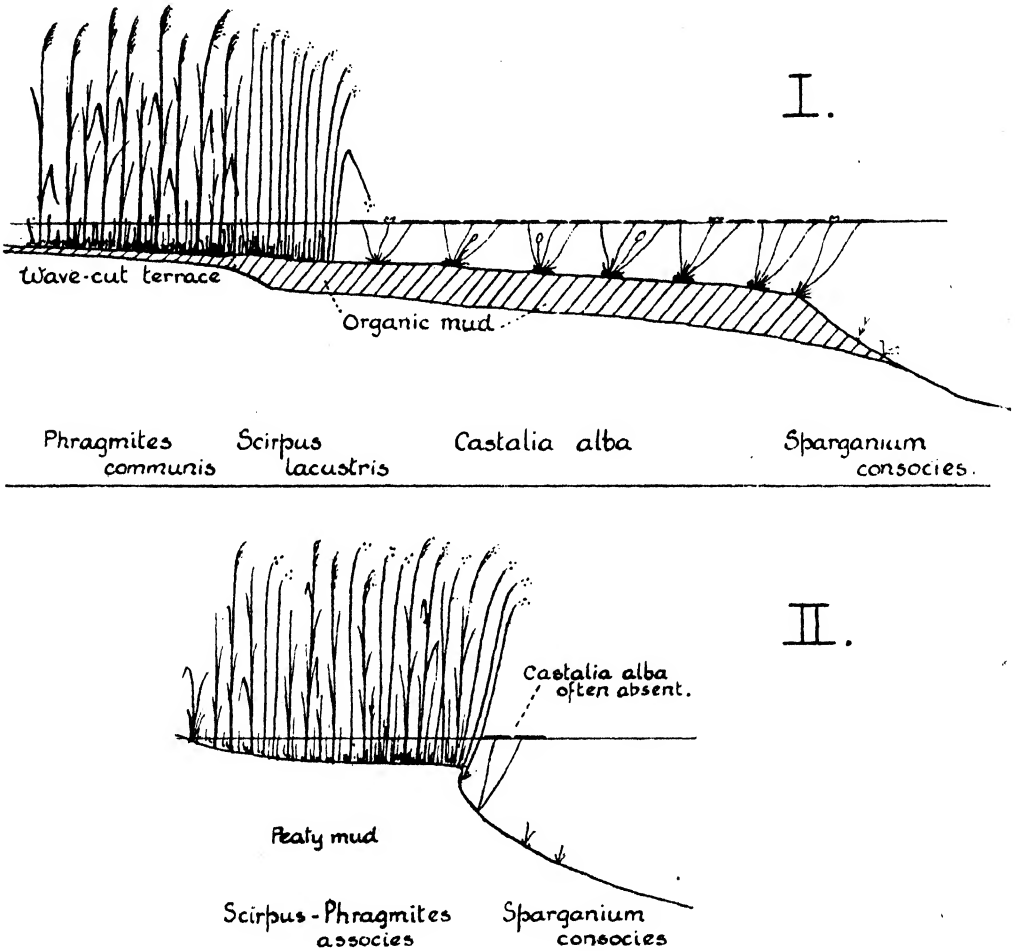


FIG. 6. I (section 2 in Fig. 5). *Castalia consociates* occupying terrace. II. *Castalia consociates* narrow or absent.

is due to wave-action being limited to the outer part of the shallow through its extent.

Fig. 7 represents a region where the silting conditions are widely different from those round Strickland Ees, for the Black Beck runs into the northern inlet and makes it the area of most luxuriant sedimentation in the lake. To the south of this area, however, there are exposed shores, where sedimentation is slight or absent, and here silting only occurs in depressions, where the

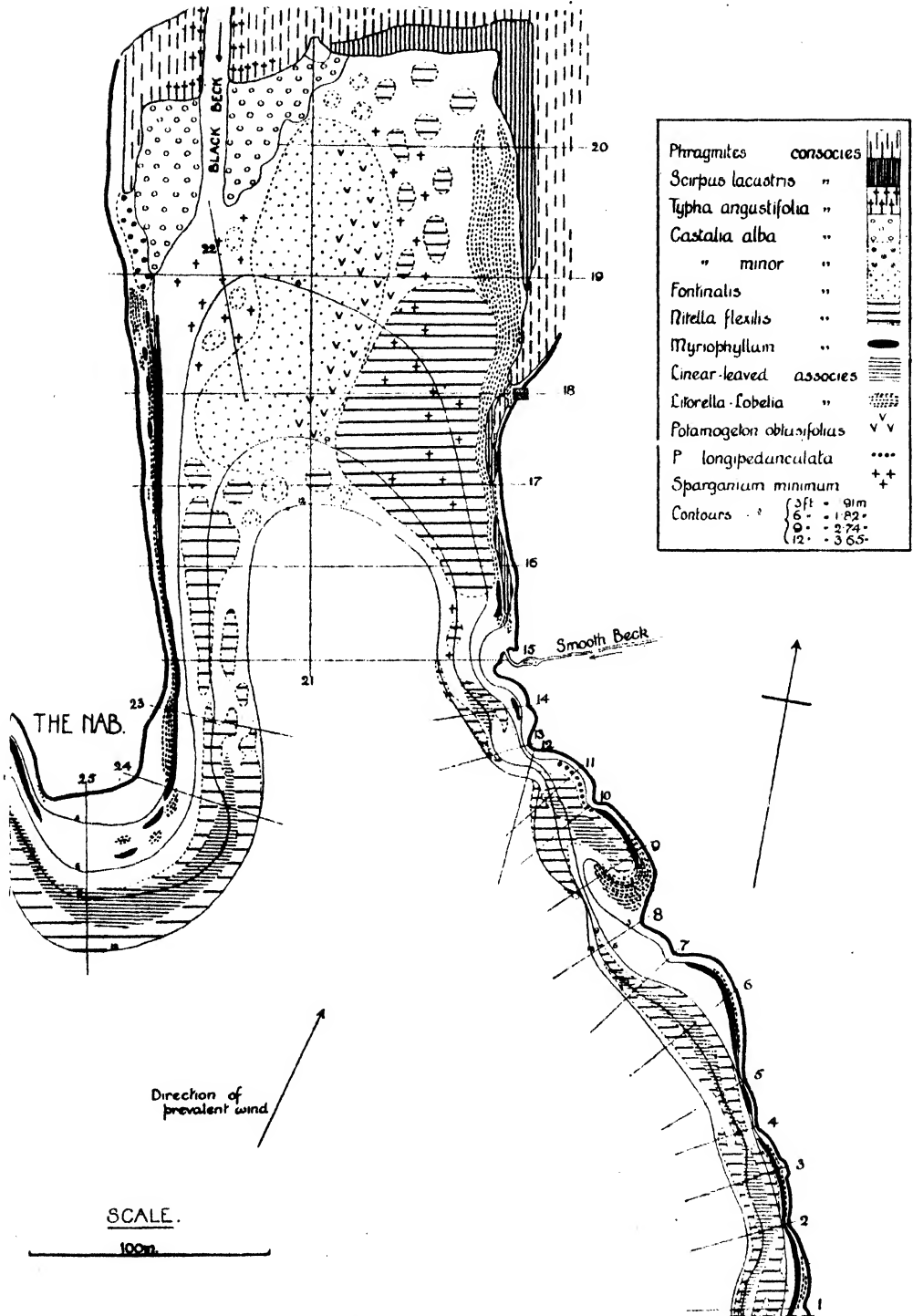


FIG. 7. Map of the aquatic plant communities round the outlets of Black Beck and Smooth Beck.

littoral current slows down. On these shores, silt is absent to a depth of 1.8 m. normally, and in the most exposed places to a depth of 2.4 m. In consequence of this, we find that the linear-leaved associates—normally in water 1.5—2.6 m. deep—is absent from depths of less than 1.8 m., and unless otherwise protected occurs at depths exceeding 2.4 m.

The only well-sheltered habitat on this eastern shore is at Sections 10 and 11. Here the linear-leaved associates extends into very shallow water, and as it has been long established, is degenerating and passing into the *Nitella* consociates. At Sections 2 and 3, however, it is clean and abundant, dominated by *Potamogeton pusillus*, and passing at Section 1 into pure *Najas flexilis*, which extends a little farther south.

On the western shore, the linear-leaved associates is passing westward round the Nab, below the region of wave-action and at depths exceeding 2.5 m. In none of these exposed stations does this associates develop great luxuriance, as it does near Strickland Ees.

Passing now to the region of very rapid sedimentation round the Black Beck mouth, we find the shores still primitive and little eroded, due to the relative shelter afforded by the Nab. But their unsilted condition is remarkable in view of the luxuriant silting in this locality. The waters of the Black Beck have normally a greater density than those of the lake, owing to the quantity of silt they contain. On entering the lake, they therefore sink and flow in a south-easterly direction, that being the line of greatest slope. Hence they deposit little or no silt on the lake shores or in places off the line of flow. The effects of this are marked. *Castalia alba*, dominant round the Beck mouth, is absent in the relatively unsilted east corner. Along the western shore, *Castalia minor*, on thin unsilted peaty mud, replaces *Castalia alba*. In the reed-swamp, *Typha latifolia* is dominant in the most silted area, and occurs nowhere else.

Among submerged communities, the silt has equally prominent effects. At Section 15, the *Nitella* consociates is degenerate (the presence of *Sparganium minimum* indicating a passage into the stage immediately preceding the advent of water-lilies), but as the map shows, it once more becomes very luxuriant to the north. This sudden re-invigoration is accompanied by a decrease in the percentage organic content of the mud, which also now yields quantities of gas on being disturbed. These two conditions are due to silting, for the proportion of gas freed grows greater as one approaches the Black Beck. There the *Nitella* consociates passes into the *Fontinalis antipyretica* consociates, but in the east corner, the *Nitella* is sparse and dirty as at Section 15.

The absence of reeds along the sheltered western shore can apparently be attributed to the lack of erosion and of silting along that shore.

The rest of the eastern shore of the lake is very regular, exposed and steep in slope; it therefore lacks both silt and vegetation. In a few localities there are traces of *Najas flexilis* or *Nitella flexilis*, but in general, the only plant

community is the line of *Myriophyllum alterniflorum* at the foot of the "mont." When the shore line becomes once more irregular and less exposed—as to the south of Elter Holme (Fig. 8)—the formation of a strong littoral current is prevented and silting develops. The conditions are sufficiently instructive to deserve notice. In this region three factors must be taken into account: (1) silting is here normally slow, most of the silt having been deposited already in the north; (2) the lake is narrow—only .22 km. across—therefore the effect of wave-action is relatively small; (3) the shore is irregular and so prevents the action of a littoral current. Thus erosion becomes the factor of greatest importance and the eroded localities show the greatest diversity of plant communities, the primitive round stones of the substratum being broken up, and silt provided. The positions in which the linear-leaved associates is found bear out this conclusion, for they are on the exposed shore of the Ees and at Sections 4 to 7, but not in the well-sheltered Ees Wyke. Reed-swamps, also, occur on the exposed and eroded shores south of the Ees and of Elter Holme, but not in the uneroded Ees Wyke.

Owing to the general scarcity of sediment in this area, the *Nitella* consociates in Ees Wyke appears never to have passed through the linear-leaved stage of the plant succession. Families of *Nitella flexilis* normally colonise stones as soon as the faintest traces of silt appear, and if silting is very slow, the substratum has no chance of developing inorganic mud (as needed by the linear-leaved associates), so that the *Nitella* consociates develops straight away. This is the normal state in the adjacent larger lakes; in Esthwaite, it is confined to the southern part of the lake in places where there is little erosion.

In this area, there is another variation in the plant succession, shown in the reed-swamps south of the Ees and of Elter Holme. The substratum of Elter Holme Bay is of gravel. Its shallowness and the sudden fall of level at the outer edge indicate that the bay is an extensive wave-cut terrace. The outermost edge of the terrace is colonised by *Scirpus lacustris*, of recent origin, since the 1888 6" O.S. shows no reeds at this place. The *Scirpus* is advancing outwards, chiefly, apparently, on its own remains, and is being succeeded by *Carex vesicaria* and *C. inflata*. *Littorella* forms a sward over most of the terrace and was probably—as is usual on loose gravel—the first colonist, now being succeeded by *Scirpus* and *Carices*. The inner part of the sward has the *Carices* largely replaced by *Castalia minor* (d.) and *Lobelia Dortmanna* (sd.), succeeding the *Littorella*. This community passes on its inner edge into a *Carex* zone in which *C. lasiocarpa* is most abundant. There is, in addition, a marginal zone of *C. elata*. Thus there are two successions from the *Littorella* sward, both ending in the *Carex* associates; the outer one (of *Scirpus lacustris* and then *Carices*) consists of plants forming a breakwater, behind which the inner succession develops a floating-leaved community. All the communities occur on black, peaty mud of over 40 % organic content, this high figure being due to the scarcity of inorganic sediment. The similarity

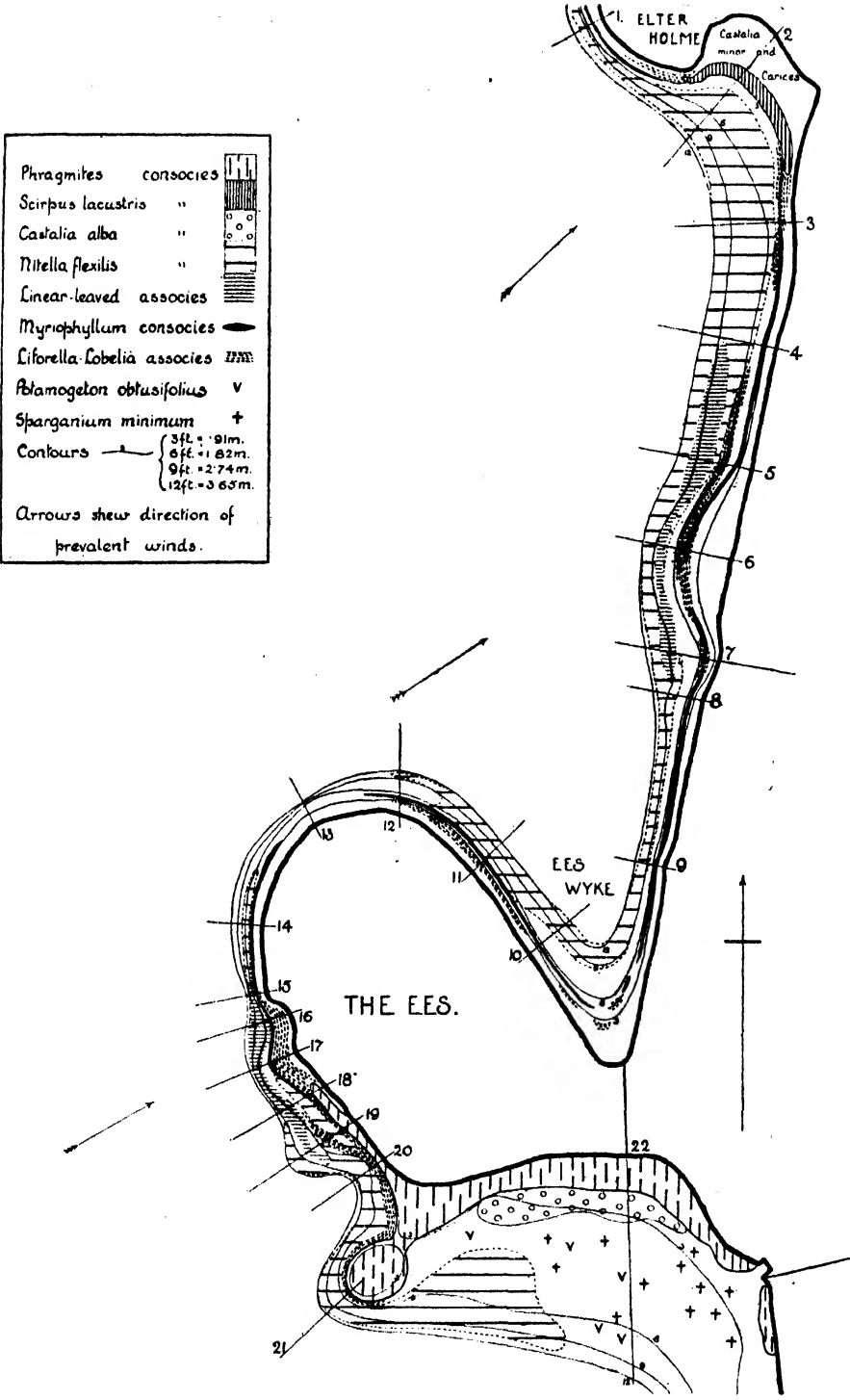


FIG. 8. Map of the aquatic plant communities round the Ees, south of Elter Holme.

of both communities and mud with those of peaty moorland tarns is very marked. I have previously pointed out that the waters of Esthwaite are of this type except for their abundant sediment.

In the bay south of the Ees, the same succession probably occurred, for vestiges of the communities still remain and the position is similar, though less exposed. Here, however, *Phragmites* and *Castalia alba* have almost replaced *Carices* and *Castalia minor*. Since the same substitution is taking place elsewhere, we are justified in concluding the *Castalia minor* consocieties and *Carex* associates to be transitory in Esthwaite, the *Phragmites* consocieties being the normal climax of the aquatic communities.

This completes the review of the typical aquatic plant communities and it only remains to summarise their relationships.

A. Communities in the region of direct wave-action.

These occur at depths of less than 1.2 m., and are hence euphotic. The substrata show transitions

- (1) from unstable to stable,
- (2) from gravel to thin, black organic mud.
- (a) Areas relatively sheltered.
 - (i) *Littorella lacustris* (*Lobelia* becoming frequent).
 - (ii) *Phragmites*.
- (b) Areas relatively exposed and kept free from inorganic silt.
 - (i) *Littorella lacustris*, (ii) *Lobelia* or *Scirpus lacustris* (in deeper water),
 - (iii) *Castalia minor* (sheltered by *Scirpus*), (iv) *Carex* associates,
 - (v) *Phragmites* consocieties.
- (c) Areas highly exposed.

These are unstable and do not permit plant growth.

B. Communities of regions at first below the direct effects of wave-action.

These occur at depths of from 1.8 to 3.65 m., and are therefore dysphotic until the *Castalia alba* stage is reached. Substrata are stable, and change from rounded stones through grey inorganic silt to light brown organic mud as the succession progresses.

- (a) Areas of relatively rapid inorganic sedimentation.
 - (i) *Nitella flexilis* families, (ii) *Najas flexilis* consocieties (5—10 %), (iii) Linear-leaved associates (10—15 %), (iv) *Nitella flexilis* consocieties (15—18.5 %), (v) *Fontinalis antipyretica* consocieties (18—19.5 %), if near streams, (vi) *Sparganium minimum* consocieties (21—24 %), (vii) *Castalia alba* consocieties (23—30 %), (viii) *Phragmites-Scirpus* associates (over 30 %).

(Figures represent humus content.)

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(b) Areas of relatively slow sedimentation.

- (i) *Isoetes lacustris* consocieties or *Nitella flexilis* families, (ii) *Nitella flexilis* consocieties, (iii) *Sparganium* consocieties (local), (iv) *Phragmites-Scirpus* associates.

C. Communities of regions between A and B.

These are euphotic and occur at depths of 0.9—1.5 m. They merge into the later stages of the above successions.

- (i) Consocieties of *Myriophyllum alterniflorum*, (ii) *Potamogeton alpinus* societies (usually in shelter), or *P. longipedunculata* societies (usually in exposed places).

In the distribution of these plant communities, silt and the organic content of the soil appear to be of greatest importance, though light intensity and shelter have also considerable influence. Silt, since it governs organic content, is probably the master factor, and shelter and exposure owe much of their influence to their effect on the rate of sedimentation. Magnin (10) states that erosion is necessary to the development of aquatic vegetation, but this is only true when fluvial sediments are absent. Then erosion becomes of prime importance. Probably the richness of the communities along the western shore of Esthwaite is in some degree due to the erosion that easterly gales have effected on the shore in winter. It will be shown next that silt is equally important in the distribution of fen vegetation.

(To be continued)

ATMOSPHERIC ELECTRICITY AS AN ENVIRONMENTAL FACTOR

BY INGVAR JØRGENSEN AND WALTER STILES

The study of the living plant and its response to environmental and genetic factors has not as yet progressed very far. Just as the struggle to acquire the necessary but preliminary knowledge of systematic botany and morphology was slow, and often hindered by the tendency to get lost in details, so the still more immense tasks which await plant physiologists and ecologists will only slowly be accomplished and in spite of similar difficulties. One of these difficulties, which is now becoming obvious, arises from the arbitrary divisions between subjects of study, and here neither ecologists nor physiologists can be regarded as having their schemes of research and fields of investigation completely mapped out. For this reason we shall here briefly deal with a recent paper by Rose Stoppel (5) where the relation between electrical phenomena and irritability has been investigated, not so much on account of the particular merits of the paper, but because it is necessary that both plant physiology and ecology should keep watchful eyes for phenomena which are likely to widen the scope of investigation in those subjects.

Livingston (3) has well said that many terms in current use in plant physiology serve principally as cloaks for ignorance. The word "irritability" must certainly be included among these.

The tendency, at any rate in this country, has been to surmount the difficulty by neglecting it, and trying to forget that irritability phenomena exist. The few investigators who have attempted to break new ground in this field cannot be said to have met with much encouragement from plant physiologists. Similarly in ecology, irritability phenomena have scarcely been recognised as having any connection with that study, and yet such universal phenomena must surely be of importance, and perhaps of vital importance, in the responses of the living plant to its environment.

As regards atmospheric electricity, in earlier years, before the time of specialisation in scientific studies, when scientists, or philosophers as they called themselves, were engaged in a preliminary survey of natural phenomena, observations on atmospheric electricity and its relation to plant growth

occupied a very prominent position in scientific investigation. To the modern specialist it is rather astonishing to realise the power of observation of these philosophers in the absence of any but the scantiest guiding fundamental principles. Thus to give one example of many which could be taken from eighteenth century writers, we may quote from Father Giambattista Beccaria, Professor of Natural Philosophy in the University of Turin (1).

“With regard to atmospheric electricity, it appears manifest that nature makes an extensive use of it for promoting vegetation.

1st. In the spring, when plants begin to grow, temporary electric clouds begin to appear, and pour down frequent electric rains. The electricity of the clouds and of rain increases afterwards in summer, and continues to do so till that part of the autumn in which the last fruits are gathered; so that it appears that the electricity which obtains in clouds and rain, when carried to a certain degree, serves to promote, with regard to vegetation, the effects of common heat.

2nd. It even seems that electricity successively supplies common heat itself with that moisture by the help of which it actuates and animates vegetation, which, if heat acted alone, would inevitably be stopped. In fact, it is the electric fire that gathers the vapours together, forms clouds with them, and afterwards dissolves them into rain. It is the same fire, therefore, that supplies the earth with the nutritive moisture which is necessary to plants, and this moisture, by melting the terrestrial saline particles it meets with, by diffusing them, along with itself, into the inmost pores of plants, causes them to grow and vegetate with such admirable and incomprehensible regularity.

3rd. The common saying of countrymen, *that no kind of watering gives the country so smiling a look as rain*, may be explained on the same principle. The rainy clouds, by extending their own electric atmospheres to plants, dispose the pores of the latter to receive with greater facility the liquid which is soon to follow; and the surrounding drops penetrate into them the better, as every one of them carries along with it a portion of the penetrating dilating element.

I know that the regular distribution of water which is made by rain also contributes to render it particularly useful. It even seems to me that to each season belong kinds of rain more or less lasting—more or less sudden—and falling in larger or lesser drops, according to the different kinds of vegetation which, in every season, are to be promoted. Now, do not all these differences chiefly proceed from the different degrees of the electricity which such rains distribute or rather accompany? I have the knowledge of many facts which are favourable to these views.

Besides, the mild electricity by excess, (positive electric action of low tension,) which, as I have observed for these many years past, constantly prevails when the weather is serene, certainly contributes to promote vegeta-

tion, in the same manner as experiments have shown us that this is likewise the effect of artificial electricity *without sparks*. And is it not likely that the former kind of electricity promotes vegetation still better than the latter can do, since nature increases it and lessens it in such circumstances and in such times as particularly require it?"

It is interesting to note that in this country also a very large number of people devoted attention to this question in these earlier days, and many writings are to be found in the literature of the earlier half of the nineteenth century which are no less ecological in their outlook than that of Beccaria from which we have just quoted. The following passage, to take an example, is taken from an interesting paper by William Sturgeon, Lecturer at the Manchester Institute of Natural and Experimental Science, published in 1846 (6). "Clouds highly charged being endowed with a formidable repulsive force, act at a great distance, and at all times of the year. In the spring and summer months, they are often productive of lightning, and teem out heavy rains, which bring down immense quantities of electric fluid to the ground, and occasion those smiling looks and healthy changes in vegetation which no ordinary showers ever produce."

It is unnecessary to multiply references to the numerous earlier writers who have recorded observations which bear on atmospheric electricity as an environmental factor. Before, however, dealing with the question of atmospheric electricity itself we may perhaps point out that in our own time Tubeuf, for example (7, 8), has dealt with certain effects of atmospheric electricity on forest trees, which may be of ecological significance, while Gager (2) has called attention to an allied question, namely, that of radioactivity as a factor in the environment of the plant.

The study of atmospheric electricity forms at present a branch of meteorology and pure physics undergoing rapid development. The huge amount of empirical material obtained from observations through centuries is being critically examined, theory after theory has been put forward, methods have been devised and systematic observations have been initiated, and it seems likely that out of the present apparent chaos there will arise a science with definite principles based on definite facts.

Apart from the elementary facts which present themselves in thunderstorms, where the lightning indicates that *potential differences* exist between different clouds or between clouds and the earth, it was soon discovered that such potential differences not only exist in thunderstorms but also in fine weather. The potential of the air is in the majority of cases (more than 90 per cent.) higher than that of the earth. This potential difference between the air and the earth is the greater the higher the point whose potential is being measured is above the surface of the earth. Points at the same height above the ground have the same potential, that is, the electric field of the earth above flat ground has the lines of force vertical, while the

equipotential surfaces are horizontal planes. Further, the field is homogeneous, or in other words the potential is a linear function of the height¹.

The intensity of the electric field is generally expressed by the potential gradient, that is, by the increase in potential per metre distance measured in volts per metre. The potential gradient in *absolute units* is obtained by multiplication by $\frac{1}{3} \times 10^{-4}$. The potential gradient is of the order of magnitude of 100 volts per metre, but it undergoes considerable daily and seasonal variation, and its relation to the various astrophysical and geographical factors is still rather obscure, although records are being made at numerous meteorological stations all over the world with the object of eliminating locally explicable variations.

Potential gradients are measured by exposing at the desired height, and insulated from the ground, a 'collector,' which may take the form of a flame, a plate covered with a radio-active substance, a water jet or a photoelectric active body, etc., which rapidly assumes the potential of the surrounding air. When the collector is connected to an electrometer this will indicate the potential to be determined.

Another fundamental characteristic of the electrical properties of the atmosphere is exhibited by its conductivity, which means that a charged body insulated from the ground gradually loses its charge. Although this was experimentally proved by Coulomb in 1785, it was first realised after the researches of J. J. Thomson and his school that the air contains charged particles which are responsible for this phenomenon. These charged particles are called ions and are characterised by the ratio between their electric charge and their mass. It is generally assumed that the charge of all ions is the same and identical with that of electrolytic ions, electrons of cathode rays, β rays in radio-active substances. The following types of ions are known according to their mass: (1) electrons with a negative charge and a mass of about $\frac{1}{2000}$ of that of the hydrogen atom; (2) atom ions with a mass of the order of magnitude of that of an atom or molecule; (3) ions with a mass many times that of an atom or molecule. It is these last which are of importance in atmospheric electricity, as electrons and atom ions are only observed in rarefied gases. It is assumed that the ionisation of a gas consists in the separation of an electrically neutral gas molecule into a negative electron and a positive atom ion, and both attach themselves very quickly to uncharged molecules and thus form the ions of the atmospheric electricity. The ions are further characterised by their specific velocity (that is, the velocity with which they move in an electric field of intensity 1 volt per centimetre).

Among the chief factors which produce ions in the atmosphere are radio-

¹ At higher levels of the atmosphere this law becomes only approximately true, the potential gradient decreases with increase in the distance from the surface of the earth, approximately to the extent of 1 volt per 10 metres. To explain this one must assume both a negative charge on the earth and a positive charge in space.

active substances in the ground and in the air and ultraviolet radiation from the sun.

The *conductivity* of the air, which is dependent on the presence of the ions, undergoes similarly to the potential gradient diurnal and seasonal variations, but generally in the opposite direction. The order of magnitude of the conductivity is 10^{-4} absolute units. The potential gradient and conductivity together condition a current whose magnitude is of the order 10^{-16} amperes per sq. cm. as it is the product of potential gradient and conductivity.

The above considerations on atmospheric electricity are necessary for a proper understanding of R. Stoppel's paper on the sleep movements of *Phaseolus multiflorus*. This author's recent work is a continuation of her earlier investigations (4) in which she concluded that the periodicity was due to autonomous action as she could not correlate the movement with any external factor. In the present investigation she attempts to control as many external conditions as possible in order to see which is responsible for the rhythmic movement. To that end the seeds were germinated in a dark room and the experiments were performed with the etiolated plants in the dark at an approximately constant temperature and in an atmosphere of approximately constant humidity. The movements of the leaves were registered by means of a self-recording apparatus. Although individual curves so obtained vary among themselves to some extent they agree in exhibiting a regular twenty-four hour periodicity, the leaves occupying their lowest position in the early morning. Experiments carried out with 25 plants during 67 days gave the following result in regard to the hour of the lowest position of the leaves.

Approximate time of lowest position	Number of days
10 p.m.	2
12 midnight	3
2 a.m.	3
3 "	18
4 "	24
5 "	13
6 "	3
7 "	0
8 "	1

From this it will be observed that in the majority of cases the leaves occupied their lowest position between 3 and 5 a.m.

Experiments on the influence of temperature showed that small variations (2° C. or more) do not influence the curve of movement at all, while sudden big variations in temperature (7° C. or more) decrease the capacity for movement, produce erratic movements, or injure the plant, but she concludes that temperature changes cannot be responsible for the periodicity.

The same holds for the influence of gravity. Although the form of the normal curve was influenced, the daily periodicity could not be produced by variation in the force of gravity acting directly. The proposition that

the periodicity was fixed in the present plant, exists latent in the seed, and again appears in the leaves of the daughter plant, she rejects after experiments with plants grown from seed obtained from different parts of the world (e.g., Java, America) where the daily variations in external conditions are different. Such plants gave similar curves to plants grown from European seed.

Having thus eliminated light, temperature, humidity, barometric pressure and gravity, and also hereditary factors, our author comes to the conclusion that the only periodically acting factor which could be responsible for the leaf movements is atmospheric electricity.

Of the two variable factors, potential gradient and conductivity, only the latter could be of importance in Stoppel's experiments, which were carried out in a closed space where no appreciable potential gradient could be found, but curves of diurnal variation in electrical conductivity of the air and those representing the daily leaf-movements of *Phaseolus* showed a striking similarity, both exhibiting a maximum about 4 a.m., or actually the conductivity was at a maximum when the leaves occupied their lowest position. It is to be regretted that the author did not make any measurements of atmospheric electrical conductivity in the room where she performed her experiments, but simply relied on the compilations from meteorological stations. Her further experiments bring out however that electrical conditions do actually influence the sleep movements considerably. The normal movement curves of leaves are much disturbed simply by touching the pot and the leaves, or by insulating the pot from the earth by means of a glass plate. These disturbances are much greater if the plants are not only insulated from the earth, but surrounded by an insulated metallic network. If the plant and pot are charged by means of a galvanic cell the regularity of movement reappears. If the surrounding insulating network is charged positively the leaves perform their normal movements, but with negatively charged network there are disturbances in the regularity of the movement curves and also in the intensity of the movement.

The same experiments performed with green plants, although the normal movement curves of the leaves are somewhat different, gave identical results. Certain experiments were carried out with artificial ionisation of the atmosphere, but it is to be regretted that no quantitative measurements were made.

So the author concludes that leaves of *Phaseolus multiflorus* respond to disturbances of the electrical equilibrium of the plant by movements of the leaves. It does not matter whether this disturbance of equilibrium is caused by touching the plant, by insulating it or by removing an insulation, or by adding a static charge. She has therefore become convinced that it is processes of an electrical nature which regulate the rhythmic leaf-movement. There must therefore be a rhythmically altering electrical stimulus which

acts on plants; this she contends is the periodically changing conductivity of the atmosphere as has already been pointed out.

The author has a theoretical part to her paper in which she draws far-reaching conclusions as to the importance of various processes for the production of potential differences in the plant and between the plant and its surroundings, and she also infers from the periodicity of a number of plant processes that they are caused by variations in atmospheric electricity. However an enormous amount of experimental work is required to enable such theories to be properly discussed.

Nevertheless, in spite of the many failings of the paper, the author has successfully shown that atmospheric electricity may have a profound influence on certain vital processes of the plant. Under these circumstances it is obvious that atmospheric electricity, as the older investigators imagined, is to be included among the environmental factors affecting the life of the plant, and as such it will have to be reckoned with in ecology.

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THE ESTABLISHMENT OF DESERT PERENNIALS

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A great deal has been written regarding the adverse conditions that must be met and withstood by desert vegetation, but the investigations on this subject have centred almost wholly in the behaviour of the full-grown plant. It requires only a brief acquaintance with the desert to realize that the adversity of physical conditions which is so important to the adult plant also exerts an extremely important influence with respect to the establishment of new individuals in a desert plant population. The object of this paper is to present a record of seven years of observation on the establishment of seedlings of four common species on a small area.

The plat which has been under observation is 557 square metres in size, and is located on the north slope of Tumamoc Hill, near the Desert Laboratory, at Tucson, Arizona. The surface of the area is inclined to the north at an angle of about 8°, and is thickly strewn with basaltic rock fragments. An abundance of very fine clay lies between and under the rocks to a depth of 20 to 30 cm., below which there are successive alternating layers of soil and hard-pan, or "caliche," and finally the rock in place. The vegetation of this area at the commencement of observations in May 1910 was made up of the following large perennials: 24 *Covillea tridentata*, 22 *Parkinsonia microphylla*, 10 *Acacia paucispina*, 9 *Opuntia versicolor*, 6 *Fouquieria splendens*, 3 *Opuntia toumeyii*, 3 *Lycium berlandieri*, 2 *Carnegiea gigantea*, 2 *Krameria glandulosa*.

In addition to the above plants there are numerous small bushes, root-perennials, perennial grasses and ephemeral herbaceous plants in season. The presence of so many large plants affords numerous areas of partially shaded ground, and the slight variability of the rock cover and the depth of the soil adds further diversity to this small area, presenting slightly dissimilar conditions for seedlings.

The writer has previously described the character of the march of climatic conditions at Tucson¹, showing that the two rainy seasons of late winter and mid summer are responsible for increases in the moisture content of the soil, and that the fine texture of the soil causes an extremely slow fall of the soil moisture during the two intervening periods of great atmospheric aridity.

¹ Shreve, Forrest. "Rainfall as a Determinant of Soil Moisture." *The Plant World*, 17, 9-26, 1914

The writer has also described the results of the first year's observation on the fate of the seedlings of *Parkinsonia* on the area in question¹, showing that some seedlings die in the two humid seasons and that a much greater number die in the arid seasons. In the continuation of this work no further attempt has been made to keep track of the particular season at which the greatest mortality of seedlings occurs.

The germination of all perennials in the Tucson region takes place during the first week following the first heavy rain of the summer season, no matter at what time the seeds may have matured. Germination commences very promptly and growth proceeds with great rapidity. On the second morning after the first heavy rain it is possible to see abundant evidences of germinative activity, and on the third morning it becomes possible to identify the young seedlings. The briefness of the germinating period makes it easy to enumerate the entire crop, as no germinations have been detected with certainty in the later weeks of the rainy season. The year of germination of each seedling has been recorded by placing a small numbered stake near it. Several times a year the area has been examined and the stakes removed from dead seedlings and recorded.

Germinations have been followed only in the case of *Carnegiea gigantea*, *Echinocactus wislizeni*, *Parkinsonia microphylla* and *Fouquieria splendens*. It was found impossible to keep a satisfactory record of the germinations of the several species of *Opuntia* owing to the abundant vegetative multiplication of *Opuntia leptocaulis*, a slender bush with numerous very short joints. These joints fall from the plants in large numbers during the arid seasons and, if they survive, take root in the next rainy season, at first closely resembling seedlings of the same species.

Carnegiea gigantea.

This plant is a massive columnar cactus, commonly reaching a height of 6 to 10 m., and usually having several branches, borne 3 to 5 m. from the base. Although there are only two plants of *Carnegiea* on the observational area, there are numerous others in the immediate vicinity. Even these two plants are responsible for the production of many thousands of seeds every spring. On establishing the observational area in 1910 a single seedling of *Carnegiea* was found, which in 1913 was 1.5 cm. high and 2.1 cm. in diameter. In 1917 this seedling is still alive and has a height of 3.5 cm. and a diameter of 4.0 cm. The fact that it has increased only 2 cm. in height in four years indicates the extreme slowness with which individuals of *Carnegiea* are established, and confirms the earlier observation of the author, based on the acceleration of growth in somewhat larger plants².

¹ Shreve, Forrest. "Establishment behavior of the Palo verde." *Plant World*, **14**, 289—299, 1911.

² Shreve, Forrest. "The influence of low temperatures on the distribution of the giant cactus." *Plant World*, **14**, 136—146, 1911.

Careful search of the observational area during the period of germination for seven years has failed to discover a single additional seedling of *Carnegiea*. Even if it were granted that seedlings had been totally overlooked in their first summer, they should at least begin to become conspicuous after two or three years' growth. It might easily be true that a few germinations had taken place and had been overlooked, but the fact remains that the seven-year period of observation has terminated with the one visible seedling found in 1910, the age of which at that time was probably from three to seven years. During the years in which the author has been interested in the establishment of desert plants a careful outlook has been maintained for all very small individuals of *Carnegiea*, and the total number less than 5 cm. high that have been seen in the course of field work is four. Their scarcity may be taken to mean either that this cactus is not maintaining its numbers, as was indicated by the earlier work last cited, or else that plants as much as 3 to 5 cm. in height have passed the age of vicissitudes and are reasonably sure to grow to adult size. While the mortality among large individuals is very high, it is rarely that a plant from 1.5 to 2 cm. in height is seen to have died or to have succumbed to the mechanical agencies that kill, break or overturn the large ones. The number of establishments necessary to maintain an adult population of a slow growing and long-lived plant is very small. If seedlings of 3 to 5 cm. in height have become so well established that a very low percentage of them die, it is easier to understand the scarcity of the seedlings without forecasting a diminution in the population.

Echinocactus wislizeni.

This is a very stout cylindrical cactus, with a diameter of 40 to 60 cm. and a height of 1 to 2 m. in full-grown individuals. The history of *Echinocactus* on the observational area is very similar to that of *Carnegiea*. A single seedling was found in 1910, the height of which in 1913 was 4.0 cm., the diameter 6.0 cm. In 1917 this plant is 11.0 cm. in height and 12.0 cm. in diameter. No other germinations in *Echinocactus* have been detected, and no seedlings have been found. The rate of growth of this plant is apparently somewhat more rapid than that of *Carnegiea*. The populations of the two have about equal density throughout the desert in general, although they are not always equally abundant, nor even invariable associates.

Parkinsonia microphylla.

Parkinsonia is a small leguminous tree with green trunk and limbs and a profusion of short thorny twigs, bearing extremely small leaves (*leptophylls*). A seed crop is borne by *Parkinsonia* only in those years with a wet or a very cool spring, and the seeds must lie in the ground at least a year before they are capable of germination. The heavy wax coating which retards their germination may be removed from fresh seeds by filing or by rinsing in ether, and is

apparently removed in nature by bacterial action or mechanical attrition. There is no evident relation between the seed crop of a given year and the number of germinations in the following summer, but a series of years without a good seed crop eventually causes a great reduction in the number of germinations. In Table I are shown the figures for the number of germinations in each summer of the last seven years, and the number of each crop surviving year by year. The effect of a reduced seed crop is seen in the irregular fall in number of seedlings from 1910 to 1915, although the absence of seedlings in the last of these years was also partly due to deficient summer rains.

TABLE I.

Establishment of Parkinsonia microphylla

Showing the number of germinations (heavy type) and the number of survivals in each crop from 1909 to 1917. Survivors noted are those standing at close of arid fore-summer of year given. The number of germinations for 1909 includes all survivors from prior years which were living at commencement of observations in June, 1910, and dead seedlings one year old which were removed from area at that time.

Year	1909	1910	1911	1912	1913	1914	1915	1916	1917
1909	303	189	19	16	7	6	6	6	6
1910	—	542	62	35	16	4	3	3	2
1911	—	—	122	49	6	1	0	0	0
1912	—	—	—	151	24	3	3	3	2
1913	—	—	—	—	34	5	2	2	2
1914	—	—	—	—	—	7	2	2	2
1915	—	—	—	—	—	—	0	0	0
1916	—	—	—	—	—	—	—	29	5
1917	—	—	—	—	—	—	—	—	38
Total number of germinations on 557 sq. metres in 9 yrs.									1226
Total number of survivals									19
Total number of germinations in the best years (1910, 1911 and 1912)									815
Total number of survivals from the best years									4
Percentage of total survivals to total germinations									1.6 %
Percentage of survivals to germinations in good years									0.5 %

On establishing the observational area in May, 1910, a number of living seedlings were found, and also a number of dead ones, some of which were slender and yellow while others were stout and blackened. The stout and blackened ones are disregarded in this table, but the slender yellow ones are regarded as the dead ones of the crop of 1909. The figure 303 for 1909 includes then, the dead germinations of that summer's crop and also the living seedlings of 1909 and of preceding years. The first line of the table refers to the entire series of seedlings of 1909 and earlier years. This population is of mixed age, undoubtedly representing the survivors of a long series of years. It has undergone no losses for the past four years, indicating that its members have now become fairly well established. None of these plants are more than 20 cm. in height, and they are by no means beyond the dangers of an extremely dry series of seasons.

By far the heaviest mortality in a crop of seedlings occurs in the two or three dry months immediately following the rainy season in which they germinated. In the case of the exceptionally heavy crop of 1910 it will be seen

that the 542 germinations were reduced by the following summer to 62, 274 of these deaths having taken place before the end of 1910. This crop continued to suffer severe losses in 1912 and 1913, being reduced to four by 1914. These have been reduced to 2 by 1917—one survivor for each 271 germinations of seven years before. The 122 germinations of 1911 were entirely wiped out by 1915. The small crop of 34 in 1913 is still represented by two seedlings—as many as remain from the larger crop of 151 in 1912.

The total number of germinations on the observational area in the eight years prior to 1917 has been 1188, of which number only 19 have survived to the commencement of the rainy season of 1917. Six of these survivors are at least eight years old, and several of them probably much older. Five of them are only one year old and may scarcely be considered as established. The number of survivors of known age which have withstood more than one year of the desert climate is eight, or 0.9 per cent. of the total number of germinations for 1910 to 1915 inclusive.

The seasonal habits of *Parkinsonia* have been fully discussed by Edith B. Shreve¹, who has shown that there are two seasons of foliation, corresponding to the rainy seasons, and that numerous twigs die on the adult trees during the last weeks of the arid seasons. In exceptionally dry years entire limbs may die, as evidenced by their change from green to a brownish yellow colour. The seedlings lose their leaves at the close of the rainy season, usually from 10 to 20 days earlier than do the mature trees. Seedlings of three to five years in age also lose branches during periods of extreme drought. The ability of a young plant to withstand drought depends primarily on the depth and extent of the root system that it has been able to develop, which is in turn dependent on the merest chance. A seedling which happens to make its start over a large rock or over a particularly solid layer of caliche may be unable to tap the lowest pockets of soil or the crevices in the caliche, and these are the only places in which a large plant may secure enough water to endure the most prolonged periods of drought. A seedling which is unable to secure sufficient water to maintain its absorption-transpiration balance loses some of its twigs, after the manner of the full-grown trees, and its ultimate survival or death is determined by the extent to which this drought-pruning goes on before the occurrence of the next rains. A seedling which has reached a height of 20 cm. has done so by a fortunate development of its root-system, and by withstanding from 20 to 40 years of the fluctuating conditions of the desert climate. Such a juvenile tree is able to withstand the loss of a considerable number of twigs, whereas a smaller individual might, under otherwise similar conditions, succumb to drought.

¹ Shreve, Edith B. "The daily march of transpiration in a desert perennial." *Carnegie Inst. of Wash. Pub.* 197, 1914.

Fouquieria splendens.

Fouquieria is a woody plant of the Fouquieriaceae composed of a very short stem from which five to thirty straight unbranched limbs are given off at an angle of 30 to 70° from the ground. The leaves (*nanophylls*) are very mesophytic in character and appear after every rain which thoroughly wets the surface layers of the soil. The seeds of *Fouquieria* are borne very abundantly in the spring of almost every year, and are so light as to be very thoroughly distributed. The number of seedlings of this plant which appear during the few days of active germination is so great as to make it utterly impracticable to keep track of them. Several hundreds may be counted on almost any square metre of ground. The mortality among *Fouquieria* seedlings immediately after the summer rains is extremely high, not more than one in every 10,000 to 100,000 surviving to the next summer. The records which have been kept for this species have been begun with the survivors of the second summer. At the close of the rainy season, and after the loss of their leaves, it is impossible to distinguish the seedlings from the dead ones, and the former are first recognisable in the summer following, when they produce a new rosette of leaves.

At the commencement of observations in 1910 there were five young plants of *Fouquieria* on the area. Since that time 21 others have been recorded, the largest number found in any one year being five. It is impossible to know the age of the original five, and there is always a possibility that seedlings may have been overlooked until their second summer. Nothing can be said, therefore, regarding the ages of the juvenile population. In July, 1917, only seven of these plants are surviving. This is a relatively high percentage of those that reached their second summer, but an extremely small percentage of the total number of germinations.

In summarizing it is possible to state that there appear to be very few germinations of *Carnegiea* and *Echinocactus*, although the percentage of survivals among their seedlings is undoubtedly higher than among non-succulent plants. A partial observation of the behaviour of *Opuntia* spp., carried through only two years, indicated that this statement is true of them also. Seedlings of *Parkinsonia* germinate with frequency, but suffer high mortality during the first and second years and a lower rate thereafter. *Fouquieria* produces very great numbers of seedlings, among which the mortality is so great in the first year as almost to eradicate the crop. The mortality among those surviving to the second year is relatively low.

The story of the germination and survival of the seedlings of forest trees in a humid climate might duplicate very closely the account which has been given of typical desert plants. In the midst of any mature plant population the opportunities for the survival and growth of seedlings of the dominant

plants are very small. The principal factor involved in the decimation of seedlings in a humid climate, however, is insufficiency of light. In the desert there is ample room for seedlings to make their start, and all of the physical conditions are favourable for them during the rainy seasons in which germination takes place. In the arid seasons, however, the rapidly decreasing soil moisture serves to eliminate all seedlings except those that have made a strong root development in favourable spots. Other plants are to be thought of as "competing" only in so far as their demands upon the soil cause it to dry out more rapidly than it would do without a plant cover. The slowness with which perennials reoccupy old roadways and other artificially cleared areas would indicate that the low rates of establishment are due immediately to the physical conditions and not indirectly to these conditions as modified by adjacent or associated plants.

The deserts of the south-western United States are notable for the extremely slow growth of all their perennial plants (excepting *Populus*, *Prosopis*, and others that grow only near a constant supply of ground water), and for the very rapid growth of the ephemeral plants of the rainy seasons. The speed of germination is equally great in the perennials and the ephemerals. The slowness of growth, great longevity, and low rate of establishment among the perennials give the vegetation of the desert an extremely stable character.

REVIEW

Russell, E. J. "Soil Conditions and Plant Growth." (*Monographs on Biochemistry.*) Longmans, Green & Co. Third Edition, 1917, pp. viii + 243. Price 6s. 6d. net.

The active interest now taken in the subject of this work is evidenced by the fact that since the publication of the first edition in 1912 (noticed in this JOURNAL, 1, p. 203), a second impression, a new edition, and now a third edition, have been called for. The subject is of enormous practical importance, is actively progressive at the present time and, as the author remarks, two journals entirely devoted to the soil have made their appearance since the present work was begun. Successive editions of Dr Russell's book have been enlarged to include topics which have recently come into prominence.

The principal enlargement in the edition now issued is due to a very useful chapter summarising the recent work on soil colloids. The author points out that the modern work, following on Van Bemmelen's discovery that the absorptive behaviour of soil to various salts closely parallels that of simple colloid "gels," essentially explains and extends the results of Way, Liebig and Knop, since the soil colloid absorbs the base of an added salt and thus turns out the acid radical, which combines with the base of a salt already present. While the older soil chemists held that soils acid to litmus contained an actual acid derived from plant residues and present in large quantities in peat, Cameron showed that all the phenomena of soil acidity can be explained as simple colloidal manifestations and do not require the assumption of soil acids at all. This worker showed that cotton and other absorbents behaved exactly like "acid" soils, turning blue litmus red. Baumann and Gully worked out the case of sphagnum peat in great detail and arrived at the same conclusion. Incidentally they showed that living sphagnum was almost as "acid" as the peat in its capacity to absorb the bases from salts, and argued that it required a great strain of the chemical imagination to suppose the existence of a powerful insoluble organic acid present in the living plant and capable of absorbing the bases from simple salts, though not in equivalent proportions. Harris took the view that a preferential colloid absorption of the base is involved in the case of mineral acid soils in Michigan, because the amount of acid liberated from equivalent quantities of different salts of the same acid is not the same. Daikuhara showed that, in the case of mineral acid soils of Japan and Korea, the development of acidity in the salt solution was due to an aluminium salt, aluminium being given up by the soil in an amount approximately equivalent to that of the base absorbed. This result is important because in the case of mineral soils it localises the seat of the absorption. Rindall, Oden, Tacke and Ehrenberg however have all argued in favour of definite humic acids in peat. None of their arguments is conclusive, but Truog's result that in the case of certain mineral soils *equivalent* amounts of different bases are required to neutralise the acid properties of the soil, is easier to explain by assuming the presence of an acid than by colloid adsorption. The balance of evidence is strongly in favour of colloid adsorption in the case of peat and other organic "acid" soils, but the mineral acid soils seem to require further investigation. The author shows that "pan" formation at the ground water level of permeable soils containing much organic material and poor in soluble salts is best explained by the formation of a ferrie-humus "gel." He also cites Keen's work, which shows that the curve of water loss by evaporation from soil is determined partly by the holding of the water by a colloid and partly by the fact that the water surface decreases as evaporation continues. There is competition for water between soil colloids and plants, as Ramann clearly points out in the third edition of his *Bodenkunde*, and the state of equilibrium under definite conditions is the "wilting point" of the plant as determined by the amount of

water in the soil immediately around its roots when the plant wilts. The colloid characters of the soil must have an important effect on all reactions taking place within it, and the author thinks it probable that some changes formerly attributed to micro-organisms may in reality be due to colloids. Further, the colloids influence both micro-organisms and plants and thus indirectly affect reactions taking place in the soil. And the remarkable changes observed in heated soils, and in soils stored in a dry condition, such as increase in the rate of nitrification, and in productiveness, are probably much influenced by changes in colloids.

The intimate mingling of the soil components amounts "almost to a loose state of combination, from which the separate substances are only extracted by drastic mechanical means or gentle chemical treatment. The soil colloids and the calcium carbonate appear to be responsible for the formation of the compound particles, and as soon as they are altered by treatment, first with acids and then with alkali, the particles fall to pieces, and the silt, clay, etc., can be readily separated by sedimentation processes." These compound particles cannot as yet be measured, but their existence "puts out of the question any complete quantitative interpretation of a mechanical analysis. The properties of a soil are not the sum of the properties of the separate fractions—clay, fine silt, etc.—because in a normal soil these fractions, which we may regard as the ultimate particles, are largely bound together into compound particles." The compound particles can be disintegrated by various cultivation methods, such as ploughing the soil when wet, or by allowing the stock of organic matter and calcium carbonate to fall too low, and can be reformed by careful cultivation and by adequate additions of organic matter and calcium carbonate, though this process may take years. The formation of these compound particles is a colloidal phenomenon. If we regard the mineral particles as the skeleton of the soil we must look upon the colloids as clothing it in many of its essential attributes. The simplest view, in accordance with all the known facts, is that the mineral particles, especially the fine silicate particles, are coated with a colloidal complex containing silica, alumina, ferric oxide, alkaline bases and phosphoric acid, derived from the weathering of the rock material, and the so-called humus. These various components are not in true chemical combination but in a state of absorption, or solid solution. The American doctrine of "the soil solution," as put forward by Whitney, wholly differed from this view, but Cameron's more recent exposition approaches more closely to it. This brief summary of Dr Russell's chapter will suffice to show the enormous importance of the study of colloid behaviour from the standpoint of the ecologist.

Of the remaining chapters the most interesting to the ecologist are those dealing with the biological conditions in the soil, the relationship between the micro-organic population of the soil and the growth of plants, the soil in relation to plant growth, and soil analysis and its interpretation. The author accepts Pickering's well-known Woburn experiments as proving that one plant may exercise a toxic influence on another growing alongside it, though there is no evidence that plants excrete toxins which remain in the soil from one crop to the next. Toxins may however exist in "sour" soils, badly aerated or lacking in calcium carbonate. The author gives a good account of the relation of bacterial numbers in the soil to various factors and to the production of ammonia and nitrates, and an excellent summary of the recent work, initiated and largely developed by himself, on the effect of soil protozoa on the bacterial population and on the results of partial sterilisation. The chapter on the soil in relation to plant growth summarises the effects of the various soil conditions on the growth of plants, and the final chapter on soil analysis and its interpretation brings out by means of a very useful consideration of special cases the strikingly different effects of various mixtures of the mineral fractions composed of particles of different size, and of the underlying of one type by another.

Dr Russell's work is characterised not only by thorough acquaintance with the history of the subject and with current work, and by an easy and lucid exposition which always concentrates on essentials, but also by a broad view and an openness of mind which make his work of special value to all who are interested, whether practically or theoretically, in the problems involved. It should be in the hands of all ecologists, not only as the most modern exposition of our knowledge of the subject, but also because almost every page suggests fruitful lines of work.

A. G. T.

NOTICES OF PUBLICATIONS ON FOREIGN VEGETATION

NEW ZEALAND VEGETATION

Cockayne, L. and Foweraker, C. E. "Notes from the Canterbury College Mountain Biological Station. No. 4. "The Principal Plant Associations in the immediate vicinity of the Station." *Trans. New Zealand Inst.* **48**, 1916, pp. 166-186, 2 plates.

The Canterbury Mountain Biological Station is situated at Cass on the eastern side of the dividing range of the South Island of New Zealand and outside the western area of heavy rainfall. In this region the principal plant formation is grass tussock.

The present paper, which is a valuable contribution to the literature of New Zealand plant ecology, contains descriptions of the principal plant associations in the vicinity of the station. The authors describe these under the headings forest, shrubland, grassland, swamp, rock, and river-bed, which classification they admit to be faulty on account of its being based partly on growth forms and partly on habitat.

1. Forest is poorly represented on account of unfavourable ecological conditions. In the small pieces examined, all situated in gullies, *Nothofagus cliffortioides* is the only tree. On it are the woody hemi-parasites *Elytranthe flavida* and *E. tetrapetala*. The undergrowth consists mainly of the small fern *Blechnum penna marina* and the erect or straggling bushes *Coprosma parviflora*, *C. microcarpa*, *Aristotelia fruticosa*, *Clematis marata*, and *Rubus subpauperatus*. On the margins of the streams, however, several other plants occur.

2 a. *Cassinia* open shrubland occurs on ground formerly occupied by tussock grassland which has been partly destroyed by burning and grazing. The shrubs grow singly or in clumps and the original tussock association occupies the interspaces. The shrubs present are *Cassinia fulvida* (dominant), *Discaria toumatou*, *Hymenanthera dentata alpina*, *Leptospermum scoparium*, *Corokia cotoneaster*, *Gaultheria depressa*, *Styphelia Colensoi*, and *Dracophyllum uniflorum*. 2 b. *Discaria* thicket consists almost entirely of the spinous semi-divaricating *Discaria toumatou*, of an average height of 1.2 m. *Clematis marata* may be fairly common as a liane. 2 c. *Leptospermum scoparium* thicket occupies fairly wide areas near the biological station. 2 d. River-terrace and debris scrub occupies such positions as the sides of gullies, faces of river terrace and stony debris of hillsides. These scrubs are usually dense owing to the abundance of the divaricating growth form. Species of this habit present are *Pittosporum divaricatum*, *Discaria toumatou*, *Aristotelia fruticosa*, *Hymenanthera dentata alpina*, *Corokia cotoneaster*, *Coprosma propinqua*, *C. parviflora* and *Olearia virgata*. Other shrubs generally present are *Gaultheria rupestris*, *Veronica salicifolia*, *V. communis* and *V. Traversii*. In wet ground *V. buxifolia odora* may be dominant. Various ground plants

are present such as *Cystopteris novae-zealandiae*, *Blechnum penna marina*, *Polystichum vestitum*, *Lycopodium fastigiatum*, *Acaena Sanguisorbae pusilla*, *A. S. pilosa*, and *Epilobium pubens*; also the lianes *Muehlenbeckia complexa*, *Clematis australis*, *C. marata*, *Rubus schmidelioides coloratus*, and *R. subpauperatus*. On Mount Sugarloaf there occurs an interesting open shrub association in which the prostrate form of *Podocarpus nivalis* is dominant. This forms broad patches while here and there are erect bushy shrubs of another variety of the same species. Other shrubs and various herbs are also present.

3. Low tussock grassland is the formation best adapted to the climate in the vicinity of Cass. It is the most important formation not only at Cass but in the South Island of New Zealand east of the great dividing mountain range. At the present time it is changed by burning and grazing but the authors conclude that in its primitive condition the tussocks (*Festuca novae-zealandiae* is the dominant species) would generally touch, while *Discaria toumatou*, *Carmichaelia subulava*, *Aciphylla squarrosa* and *Agropyrum scabrum* would be plentiful. On the other hand the small tussock *Poa Colensoi* and a number of herbs and semi-woody plants now common would be far less abundant. Introduced plants play but a small part in the present association. Nor is it expected that they will increase. "The truth seems to be," say the authors, "that a balance has been reached and that a plant association unknown in primitive New Zealand is now well established."

4. Swamp at Cass belongs to the class "reed swamp" and to the association where *Typha angustifolia Muelleri* is dominant. The vegetation exhibits girdles according to the depth of water. Near the open water is *Typha*; next a girdle in which *Carex secta* is dominant, and associated with it are *Phormium tenax* and *Carex Gaudichaudiana*. At the margin of the swamp is a considerable assemblage of herbaceous plants.

5. Lists are given of plants occupying "montane rock" and "subalpine rock." These habitats are not sufficiently defined and most of the species enumerated belong equally to other associations.

6. River bed includes both the unstable stony river bed and the older stable flood plain on either side. These are occupied by quite distinct associations though not well defined in the vicinity of Cass. On unstable river bed there are *Epilobium melanocaulon* and mats of *Raoulia tenuicaulis* and *R. australis*; also there may be tussocks of *Festuca novae zealandiae*. On river terrace recently formed there are present besides the species already mentioned the following mat or cushion plants: *Muehlenbeckia axillaris*, *Acaena inermis*, *A. microphylla*, *Raoulia Haastii*, also rosettes of *Geranium sessiliflorum* and the prostrate shrub *Discaria toumatou*. On long established terrace humus has been added to the soil and various species of other plants occur. As the humus content increases *Festuca novae zealandiae* appears and gradually low tussock grassland is established.

The paper is illustrated by photographs and there is appended a list of species belonging to the associations described.

W. R. B. OLIVER.

Bird, J. W. "Observations on the Lianes of the ancient Forest of the Canterbury Plains of New Zealand." *Trans. New Zealand Inst.*, **48**, 1916, pp. 315-353, 4 plates, 10 text figs.

This is a valuable paper on New Zealand plant ecology involving a lot of careful work. The author takes for study the following 12 species of lianes from a small piece of forest near Christchurch, New Zealand. *Rubus australis glaber*, *R. schmidelioides*, *R. cissoides*, *R. subpauperatus*, *Fuchsia Colensoi*, *Metrosideros hypericifolia*, *Muehlenbeckia australis*, *M. complexa*, *Parsonia heterophylla*, *P. capsularis rosea*, *Clematis indivisa*, *Tetrapathaea australis*. A description of the life form, leaf form, leaf anatomy, and method of gaining support, of each species is given, and illustrated with many diagrams and photographs.

The chief factors determining stem elongation are considered to be moisture and diminished light. The scrambling habit was at first the effect of these stimuli. In all lianes there is a tendency to adventitious rooting by creeping stems in moist places; and it seems probable that the nature of the environment determines whether the roots shall elongate and act as absorbing organs, or whether they shall remain comparatively small and fasten the liane to the support. Twining is of frequent occurrence not only in true lianes but also in other plants in which the twining is only slightly marked. Transitions from leaf to tendril are also common. The leaves of *Rubus cissoides* are often reduced to midribs which with their strong recurved hooks form distinct climbing organs. In New Zealand atmospheric moisture is great and the climate is equable; and this condition of affairs is probably responsible for the high development of lianes there.

Shade leaves are found to present many differences from sun leaves. The expansion of the leaf is advantageous in that a larger number of light rays fall upon the assimilating surface, while the broad palisade cells, which give the chloroplasts a more superficial position, further aid in the utilization of light. In sun leaves, as compared with shade leaves: (1) Leaf-blades are smaller and more coriaceous. (2) Petioles are shorter. (3) Lateral walls of epidermal cells are straighter than in shade leaves. (4) There is in most cases a thick cuticle. (5) Palisade tissue is well developed with the cells elongated and very closely packed. (6) Spongy tissue comprises a smaller portion of the thickness of the leaf and has small intercellular spaces. (7) Stomata are more numerous than in shade leaves.

Poppelwell, D. L. "Notes on the Plant-covering of the Breaksea Islands, Stewart Island." *Trans. New Zealand Inst.*, **48**, 1916, pp. 246-252.

The Breaksea Islands lie east of Stewart Island, New Zealand. Joss' Island is the largest of the group and its plant covering is described under the heads (1) rocks and cliffs, (2) forest, (3) heath.

Rocks and cliffs support an assemblage of shrubs, grasses and ferns varying as foothold and exposure allow. The shrub *Olearia angustifolia* is the principal plant in exposed situations. *Poa Astoni* covers the cliffs in places, and the shrubs *Olearia Colensoi* and *Veronica elliptica* occur in similar places, also the succulent plants *Mesembrianthemum australe* and *Tetragonia trigyna*. Where wind strikes less directly are patches of *Stilbocarpa Lyallii*, and at the rear of the frontal rocks *Asplenium obtusatum* and *Blechnum durum*.

Forest. The soil consists of a deep layer of peat, fairly dry, and undermined everywhere with the burrows of mutton birds (*Puffinus griseus*). The dominant tree is *Metrosideros lucida*, 8-10 m. tall, with partly prostrate trunks. Other trees present are *Griselinia littoralis*, *Pittosporum Colensoi*, *Nothopanax Colensoi*, *Coprosma areolata*, *Fuchsia excorticata*, *Rapanea Urvillei* and *Olearia Colensoi*. The undergrowth consists mainly of *Stilbocarpa Lyallii* which is very dense in places; its great leaves, spreading horizontally, exclude the light and prevent other growth. Where sufficient open space allows there are present the ferns *Asplenium lucidum*, *A. obtusatum* and *A. scleropium*. Tree trunks are covered with *Polypodium diversifolium* and *Asplenium flaccidum*.

Heath. Where the full force of the wind strikes the coast there is a considerable area of open heath. The soil is peaty and in parts fairly damp. Low stunted *Leptospermum scoparium* forms the principal shrubby vegetation. Associated with it are *Dracophyllum longifolium*, *Styphelia acerosa*, *Olearia arborescens* and cushions of *Oreobolus pectinatus*.

On Breaksea Island is an interesting association of plants on sea cliffs. In southerly weather the waves strike these cliffs and splash right over the top. Along the top practically no shrubs grow, but the grass *Poa Astoni* covers the ground. Among it grow *Myosotis albidus*, *Gentiana saxosa*, *Apium prostratum*, *Selliera radicans*, *Crassula moschata*, and some low bushes of *Olearia angustifolia* sheltering *Asplenium lucidum* and *Blechnum durum*.

Poppelwell, D. L. "Notes on the Plant-covering of Pukeokaoka, Stewart Island." *Trans. New Zealand Inst.*, **48**, 1916, pp. 244-245.

Pukeokaoka is a small island in Foveaux Strait, New Zealand. The top of the island is almost flat and supports some forest 20 to 30 feet high. This consists of *Metrosideros lucida*, *Schefflera digitata*, *Pittosporum Colensoi*, *Aristolelia racemosa*, *Fuchsia excorticala*, *Meliccytus lanceolatus*, *Nothopanax Edgerleyi*, *Griselinia littoralis*, *Carpodetus serratus* and *Veronica elliptica*. The undergrowth is 3 ft. or 4 ft. high and consists of *Asplenium bulbiferum*, *A. flaccidum*, *A. scleropitum*, *A. lucidum*, *Polystichum vestitum*, and *Polypodium diversifolium*, while the liane *Rhipogonum scandens* is common. The only tree-fern is *Dicksonia squarrosa*. Epiphytes are not common, consisting principally of the ferns *Asplenium flaccidum* and *Polypodium diversifolium*.

The remaining vegetation consists mostly of scrub, and of various herbaceous plants and ferns on the sea cliffs.

IN MEMORIAM

SARAH MARTHA BAKER

SARAH MARTHA BAKER, the only daughter of George and Martha Baker, was born on 4 June, 1887, and received her early education at home. She early showed an interest in fine art and entered the Slade School in 1905. After a short time she became more closely associated with University College, London, and entered the Science side in 1906, taking her B.Sc. with 1st Class Honours in Chemistry and Botany in 1909. In 1912 she was elected to the Quain Studentship in Botany, and except for a brief period spent at Munich in 1910, she was entirely associated with University College. In 1914 she was elected a Fellow of the Linnean Society of London, and in 1916 a member of the Council of the British Ecological Society.

It was Dr Baker's first intention to devote most time to more or less purely chemical work, and she began an investigation on the synthesis of certain members of the camphor series. During the inevitable delays in this research she began to work on the effect of formaldehyde on living plants. It was characteristic of Sarah Baker to select two such difficult problems for first investigations. She soon found, however, that it was impossible to keep both running at the same time and, as she found herself very happy in her botanical surroundings, she soon devoted all her energies to work in that field.

The investigation on formaldehyde was published in 1913 and was approved for the degree of Doctor of Science. From the purely physiological aspect, this is Dr Baker's most important published work, and although the results obtained were incommensurate with the amount of labour involved, they are of value in throwing light on an evasive subject. The paper shows the ingenuity, orderliness and clear thinking characteristic of Dr Baker. The chief result obtained was that formaldehyde is possibly a stage in photosynthesis but its condensation into sugars and other food materials requires radiant energy. She believed that formaldehyde was converted into keten (Collier's hypothesis) before elaboration into the higher organic compounds. It was not her intention to leave the subject of photosynthesis. Her experiments had been proceeding for years but were stopped by her untimely death.

She also made some interesting observations on induced morphological variation in Algae, and much time was spent on an investigation upon the parthenogenesis of the oospheres of brown Algae. The results, however, were not published. At the time of her death she was much interested in transpiration and formulated her ideas in a paper read before the British Association at the Manchester meeting in 1915. Whilst these investigations were in progress Sarah Baker showed her interest in the economic side of botany in her work on the use of enzymes in the treatment of fungus diseases. This work

was often treated as a joke, especially the attempted cure by similar remedies of a distressed goldfish unfortunately suffering from a bad attack of *Saprolegnia*. Shortly before her death she gave a very successful public lecture on Vegetable Dyes, whilst her last investigations were towards the determination of the bread-making values of various wheat substitutes.

Her country home being on Mersea Island in Essex, Dr Baker was early attracted to the study of seaweeds: it was, however, a visit to Bembridge in the Isle of Wight which first drew her attention to the zonation of the brown algae. The problem was investigated chiefly at Blakeney Point and Mersea, and the results were published in the *Journal* of the Linnean Society of London. The first part is descriptive of free growing and embedded varieties of *Pelvetia* and *Fucus*; three new varieties are described. The second part, in which Dr Baker was assisted by Miss Bohling, deals with the systematic relationships and ecology of the marsh fucoids. This work is not only Dr Baker's most important contribution to botanical science, it is one of the most important investigations of recent times upon the subject. The difficulties to be overcome may not be apparent in the published account, but those who saw the investigation in progress fully realised the amount of labour involved, labour not only mental but physical, especially in regard to the numberless tide observations required.

Of Quaker origin, Sarah Baker was of a retiring disposition; and although she did not take a prominent part in College life her quiet influence permeated it both widely and deeply. To her friends she showed no restraint and entered fully into their common interests. In spite of physical disability she was possessed of great courage and carried on where the majority would have stopped. In her work she was entirely happy; it was the commonest occurrence to hear her singing whilst at work in her laboratory. Indeed, it may with truth be said that she was never happier than when working.

As an investigator she had boundless energy, and the faculty of formulating her problems. In her early physiological work she tended somewhat to consider the plant as a test tube, but this, doubtless a reflection of her chemical training, quickly disappeared when the problems of plant life were studied in the field. Her earlier training in the fine arts finds expression in the illustrations of her published work; she was never guilty of a bad or careless drawing.

Her premature death on 29th May, 1917, is a serious loss to botany and particularly to the botany department of her College. To the few who really knew her she was the most faithful friend and the most loyal colleague.

PUBLICATIONS.

1909. "On the causes of the Zoning of Brown Seaweeds on the Sea Shore." *New Phyt.* **8**, 196.
1910. *Ibid.* Pt. 2. "The effect of Periodic Exposure on the Expulsion of Gametes and on the Germination of the Oospore." *New Phyt.* **9**, 54.
1911. "On the Brown Seaweeds of the Salt Marsh." *Journ. Linn. Soc. Lond. Bot.* 1911-12, **40**, p. 275.
1913. "Note on a new treatment for Silver Leaf Disease in Fruit Trees." *Ann. Bot.* **27**, 172.
1913. "Quantitative Experiments on the Effect of Formaldehyde on Living Plants." *Ann. Bot.* **27**, 410.
1915. "Liquid Pressure Theory of Ascent of Sap in Plants." *British Assoc. Manchester*, Section K.
1916. In co-operation with Maude H. Bohling. "On the Brown Seaweeds of the Salt Marsh. Part II. Their Systematic Relationships, Morphology, and Ecology." *Journ. Linn. Soc. Lond. Bot.* **43**, 325.
1917. Chapter on "Vegetable Dyes" in *The Exploitation of Plants*. London: Dent and Sons.

THE BRITISH ECOLOGICAL SOCIETY

MEETING AT ROTHAMSTED EXPERIMENTAL STATION
SATURDAY, JUNE 9TH, 1917

A very successful meeting was held on the above date: about twenty members of the Society were present. The day's programme was divided into two parts so as to allow those unable to be present in the morning to join later. Owing to the unavoidable absence of Dr Russell during the earlier part of the day the order of proceedings, as announced on the notices, was reversed.

The main party reached the Laboratory at 10.30 a.m., whence under the guidance of Dr Brenchley they were conducted to Geescroft Wilderness. Prior to its examination Dr Brenchley gave a short account of its history and the character of the vegetation. The area termed Geescroft Wilderness was formerly arable land but has now been uncultivated for a period of about 35 years. At the present time it exhibits a scrub condition with numerous young trees of *Quercus robur* accompanied by *Corylus*, *Acer*, etc. The most abundant species of the ground vegetation is *Aira caespitosa*, and *Festuca rubra* is also very common. The incursion during recent years of Leguminosae and the decreasing amount of *Aira* suggest a diminishing acidity possibly correlated with the lowering of the permanent water table, which is general throughout the county. Parallel changes have for instance taken place on the neighbouring Common (cf. Salisbury, *Trans. Herts. Nat. Hist. Soc.* p. 71, vol. xv.). A complete account of the two Wildernesses has already appeared in this JOURNAL (Brenchley and Adams, 3, p. 200 et seq.). To the list of species there enumerated for Geescroft Wilderness two (*Luzula albida* vr. and *L. multiflora* o.) were added as a result of the Society's visit.

Broadbalk Wilderness and the neighbouring field plots were then examined and the party had an *al fresco* lunch under the adjoining trees.

In the afternoon the extremely interesting object lessons afforded by the Grass Plots were demonstrated by Dr Russell. It would be impossible in the compass of this short note to do justice even to a portion of the numerous fascinating problems here afforded (see A. D. Hall, *The Book of the Rothamsted Experiments*). Perhaps most interesting of all however to the ecologist was the striking evidence of the effects of acidity on some of the plots (e.g. those manured with ammonium salts) and the profound contrast, produced by liming, on the control halves. The quantitative and qualitative differences resulting from the application of incomplete manures were clearly indicated, and in reference to the latter the large number of species on the unmanured plot offered an impressive contrast to the few present where a complete manure was supplied.

By the kind hospitality of Dr Russell the party was entertained to tea in the Laboratory, after which the new buildings were inspected.

Before leaving the President expressed the Society's keen appreciation of the kindness of Dr Russell and his Staff, which was heartily endorsed by all present.

E. J. SALISBURY,
Hon. Sec.

NEW MEMBERS

Since the publication of the last list of members the following have joined the Society:

W. H. Howarth, 61, Cecil Park, Crouch End, London, N. 8.

Dr H. Jeffreys, 199, Albany Street, London, N.W. 1.

A. A. Pearson, 3, North View, Wimbledon Common, London, S.W. 12.

Miss F. A. Randell, 37, Temple Street, Oxford.

ANNUAL GENERAL MEETING

The Annual General Meeting will be held on Saturday, December 15th, at 10 a.m. in the Botanical Department, University College, London.

I. A. R. I. 75.

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